# SPATIOTEMPORAL VARIATION IN OCCUPANCY AND PRODUCTIVITY OF GREBES IN PRAIRIE CANADA: ESTIMATION AND CONSERVATION APPLICATIONS

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# ABSTRACT

Wetlands of the Prairie Pothole Region (PPR) provide important breeding habitat for greater than 30 species of waterbirds. Approximately 70% of PPR wetlands have been lost since European settlement and remaining wetlands are subjected to frequent degradation, primarily due to agricultural activities. Horned grebes (*Podiceps auritus*) are experiencing long-term population declines and are listed as a species of Special Concern in Canada. Because there is virtually no information on the status and trends of pied-billed grebes (*Podilymbus podicep*) this species is also of considerable conservation concern.

Grebes are recorded on the Waterfowl Breeding Population and Habitat Surveys (WBPHS) conducted annually in May by the Canadian Wildlife Service; however, how accurately these counts reflect actual abundance has been unknown. Using a repeated counts method in 2010 and 2011, estimates of detection probabilities averaged 0.48 and 0.18 for horned and pied-billed grebes, respectively. These results suggest that WBPHS ground surveys may be used as an efficient and effective management tool for monitoring horned grebe abundances. However, low detection rates for pied-billed grebes lend little support for including the species in future monitoring efforts using the WBPHS. I recommend that the Canadian Wildlife Service consider implementing standardized ground survey methods to facilitate annual monitoring of horned grebe abundances.

Marshbird research has focused primarily on breeding habitat use or selection but has seldom examined how productivity is related to wetland characteristics. Understanding processes that affect distribution patterns and productivity of grebes could provide insights into actions needed to achieve conservation goals. Therefore, occupancy of wetlands by breeding and brood-rearing horned and pied-billed grebes was evaluated on 6-7 study sites (5.8-11.6 $km^2$) in south-

central Saskatchewan, 2010 and 2011, and related to wetland and upland habitat features. Wetland occupancy by grebes was influenced by interspecific competition as well as local and landscape-level wetland features. Horned and pied-billed grebes rarely co-occurred on smaller (≤4 ha) semi-permanent and permanent wetlands. At the wetland level, horned grebe occupancy and productivity were highly correlated with the amount of emergent vegetation, whereas wetland area alone was a better predictor of adult pied-billed grebe occupancy and productivity. At a landscape level, the number of semi-permanent, permanent, and artificial wetlands on each study site was an important predictor of breeding and brood-rearing wetland occupancy probability for horned grebes in 2010 and for pied-billed grebes in both years. However, breeding horned grebe occupancy probability and productivity were higher in low wetland density landscapes in 2011. Horned grebes may be opportunistic, exploiting more of the available wetland habitats in low wetland density landscapes during years of above-average water conditions. Conservation initiatives for grebes should consider the roles of wetland-specific and landscape-level features while protecting semi-permanent and permanent wetlands in landscapes characterized by both high and low wetland densities.

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# CHAPTER 1. GENERAL INTRODUCTION

The Prairie Pothole Region (PPR) of North America is characterized by millions of post-glacial depressions that have created a dynamic wetland ecosystem subject to annual and seasonal shifts in water regimes and vegetation structure and distribution (National Wetlands Working Group 1999). PPR landscapes are renowned for providing habitat for breeding waterfowl which in turn supports a disproportionately high proportion of North America's annual waterfowl production (Crissey 1969; Greenwood et al. 1995; Higgins et al. 2002). Similarly, these wetlands provide a significant proportion of the breeding habitat for >30 species of waterbird (Beyersbergen et al. 2004). The PPR has lost approximately 70% of wetlands since the pre-settlement era and many remaining wetlands are frequently subjected to high impacts and degradation, primarily due to agricultural activities (Cox 1993; Dahl 2000; Bartzen et al. 2010). As a result, many waterfowl and especially waterbird species have been negatively affected by land use practices (Beyersbergen et al. 2004).

The horned grebe (*Podiceps auritus*) is experiencing long term population declines, estimated at ~45% since the mid-1960s (COSEWIC 2009). Threats include wetland loss, degradation, and eutrophication primarily through agricultural activities, temporary loss of wetlands during drought periods, and degradation of wintering areas by oil spills (COSEWIC 2009). As a result, horned grebes have been listed as a species of Special Concern by the Committee on the Status of Endangered Wildlife in Canada (COSWEIC). Little information exists on the current status and trends of pied-billed grebes (*Podylimbus podiceps*) and no population estimate exists (Mueller and Storer 1999). Although more geographically wide-spread than horned grebes, pied-billed grebes could be experiencing long term population declines because they are threatened by many of the same factors that affect horned grebe

populations (Mueller and Storer 1999) and are thus a species of particular conservation concern (Conway 2011). Reproductive stages of the grebes' life cycles are tied to freshwater ecosystems, particularly in the prairie and parkland ecoregions, where they occupy the upper trophic levels of wetland systems. As a result, grebes may be good indicators of wetland health and change (O'Donnel and Fjeldså. 1997).

## 1.1 Ecological rationale

A central goal in animal ecology is to understand why animal abundances vary over time and space (Krebs 1972; Williams et al. 2002). Factors that affect habitat occupancy patterns of grebes are not well understood because of difficulties in obtaining unbiased abundance estimates. Further advances could be made by evaluating characteristics of productive habitats in addition to features of occupied breeding habitats. Breeding birds may be distributed so that productivity is equal across occupied habitats unrelated to density, as predicted by ideal-free distribution models (Fretwell and Lucas 1970). Density of breeding adult grebes may be a reliable signal of habitat suitability (Fretwell and Lucas 1970, Bock and Jones 2004), but a positive relationship between density and productivity does not always hold in birds (Kluyver and Tinbergen 1953, van Horne 1983, Vickery et al. 2002).

## 1.2 Conservation rationale

Understanding the processes that produce distribution patterns may also provide insights into actions needed to achieve management or conservation goals. Although counting grebes presents difficulties for large scale survey methodologies, potential exists to include horned, pied-billed, eared (*Podiceps nigricollis*) and red-necked (*Podiceps grisegena*) grebes in the Waterfowl Breeding Population and Habitat Survey (WBPHS), an annual survey conducted by the US Fish and Wildlife Service (USFWS) and the Canadian Wildlife Service (CWS). The

survey consists of an aerial count of waterfowl and wetlands, complemented by ground counts to provide visibility correction factors (i.e., to adjust for imperfect detection of birds and ponds from the air). Count data obtained via the WBPHS are intended to inform waterfowl population management decisions, particularly for mallards (*Anas platyrhynchos*). The WBPHS is timed so that it coincides with when most mallard breeding pairs have arrived on survey areas. Although grebes are recorded by ground crews on the survey, it is unknown how accurately they are counted (for example, considering detection probability).

Grebes may serve as an indicator of environmental quality due to their high sensitivity to ecosystem and habitat degradation (O'Donnel and Fjeldså. 1997). Therefore, obtaining an improved understanding of the factors that affect the abundance and distribution patterns of grebes provides new information that is needed by agencies concerned with wetland conservation or species at risk to develop spatially explicit models (i.e.: identifying suitable habitats at landscape scales within the Canadian PPR). Global climate change is predicted to increase the frequency and severity of drought in prairie Canada (IPCC 2012) amplifying the importance of identifying, conserving and restoring semi-permanent and permanent wetlands for grebes and other taxa.

## 1.3 Objectives and thesis organization

My research had two principal goals. First, in Chapter 2, I evaluate practical methods for estimating the abundance of grebe species during the WBPHS, and estimate species-specific detection probabilities. Second, in Chapter 3, I investigate how grebes are distributed over time and space to provide new insights into the factors that govern wetland occupancy, distribution, and productivity patterns in the Canadian PPR.

# CHAPTER 2. SURVEYING POPULATIONS OF BREEDING GREBES IN PRAIRIE CANADA: ESTIMATION PROBLEMS AND APPLICATIONS

## 2.1 Introduction

Management of harvested North American migratory birds is supported by a suite of monitoring programs that are designed to inform decision-making and sustain waterfowl populations (Nichols et al. 1995). For example, the United States Fish and Wildlife Service (U.S. FWS) and the Canadian Wildlife Service (CWS) conduct annual midcontinent Waterfowl Breeding Population and Habitat Surveys (WBPHS) to estimate annual abundances of breeding waterfowl. By contrast, relatively little information exists regarding population status, distribution, and population dynamics of many non-waterfowl species, especially those that are difficult to monitor (Conway 2009). These information gaps are exacerbated for waterbirds, a group composed of various guilds of species with behaviours and habitat use patterns that do not easily allow for large scale population monitoring. Increasingly, conservation agencies are challenged to broaden their monitoring programs to assess a wide range of species and landscape changes; to facilitate this program shift, managers require fundamental knowledge about abundances and habitat associations of a wider range of avian species, including species of special concern such as certain species of grebes (family: Podicipedidae).

Horned grebes (*Podiceps auritus*) are experiencing a shift in their breeding distribution towards the northwest into the Canadian prairies as breeding grounds in the southeastern portions of its range are lost or degraded (Stedman 2000). Horned grebes have been listed as a Species of Special Concern by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) because of long-term population declines and breeding habitat loss. The designation was also issued because an estimated 92% of the breeding range of the horned grebe is located in Canada,

with the majority of horned grebes breeding in the Canadian prairies (COSEWIC 2009). The current status of horned grebes in North America is estimated to be between 200,000-500,000 individuals, representing a population decline of up to 45% since the 1960s (COSEWIC 2009); the reliably of this estimate is unknown.

Pied-billed grebes (*Podilymbus podiceps*) may be experiencing population declines due to habitat loss and degradation, suspected to be primarily due to agricultural and chemical inputs (Mueller and Storer 1999). Although the species is geographically more widespread, no population estimates are available due to the difficulty in surveying this species. Despite the lack of reliable knowledge about pied-billed grebe distributions and abundances, the Canadian PPR likely provides breeding habitat for a significant proportion of the pied-billed grebe population (Mueller and Storer 1999).

It is not known whether existing, large-scale monitoring programs such as the WBPHS could be used to survey grebes but there is growing interest in assessing whether ground survey methods could be modified to obtain annual population indices for non-waterfowl species, including grebes. Some evidence suggests that horned and pied-billed grebes have arrival, settlement and breeding chronologies similar to mallards (*Anas platyrhynchos*; Arnold 1994). Horned grebes initiate clutches between 17 May-11 June (Ferguson and Sealy 1983) in south-western Manitoba, and pied-billed grebes in south-central Saskatchewan likely have clutch initiation dates spanning early May to early June (Muller and Storer 1999). Grebes may be readily observed during the waterfowl surveys because grebes swim frequently at the water surface, are large-bodied and easy to identify when compared with smaller, cryptic, or nocturnal waterbird species that some observers may have difficulty identifying.

Knowledge about distribution and productivity patterns of grebes based on habitat data could be used to develop decision support models or integrated with existing modeling tools to guide waterfowl programs and conservation initiatives. Data collected from this study are intended to inform monitoring programs for grebes by determining appropriate survey methodologies and effort needed to detect population changes through trend analyses. Grebes have been counted consistently on Saskatchewan survey strata since 2006 (D. Nieman, Canadian Wildlife Service [retired], pers. comm., April 2010); however, how well these counts reflect actual abundance is unknown. Because the waterfowl ground survey has an imperfect detection probability for ducks (Pagano and Arnold 2007), it seems certain that the survey would under-represent abundance of grebes even when ground crews make a concerted effort to document them. If reliable grebe detection probabilities can be obtained using the WBPHS, or if they can be calculated with limited extra effort, this annual survey could provide a means to obtain relative abundance data to monitor breeding populations over time and space. Here, my main objective was to estimate species-specific detection probabilities for horned and pied-billed grebes, and assess the feasibility of incorporating abundance estimation using repeated counts procedures (Royle 2004) into the annual WBPHS to obtain unbiased estimates of grebe population sizes.

### 2.1.1 Waterfowl Breeding Population and Habitat Survey

The WBPHS was initiated in 1947 and became operational in 1955 (U.S. FWS and CWS 1987). The western (or traditional) survey area extends from South Dakota and Montana, into the Canadian prairies, through the boreal forest and tundra regions, and northwest to Alaska (Fig. 2.1). Crews in fixed-wing aircrafts conduct extensive surveys of wetlands and waterfowl on a series of segments (transects) at an altitude of 45 m. Aerial crews identify and count all duck

species observed within 200 m of each side of the aircraft. Each segment is 29 km long. Typically within 24 hr, ground crews conduct an intensive survey on a subsample of the flown segments (termed "air-ground comparison segments"; hereinafter segments) to provide visibility correction factors that are used to improve waterfowl abundance estimates (USFWS and CWS 1987). In each of the three prairie provinces, there are typically 3 ground crews consisting of 2-3 observers that survey as many as 3 segments per day. Segments are centered on roadways so ground crews document all birds within 200 m of the road. In the Canadian prairies, the WBPHS is typically conducted between 1-30 May to coincide with mallard breeding chronology. Standard Operating Procedures for the WBPHS can be found in USFWS and CWS (1987).

### 2.1.2 Estimating detection probabilities

Detection probabilities usually influence abundance estimates so they must be calculated to obtain unbiased abundance estimates (Nichols et al. 2000). The ground portion of the WBPHS is designed to provide a visibility correction factor for numbers of birds counted from an aircraft, and assumes detection probabilities are 1 (i.e., a complete census) when they are not (Pagano and Arnold 2007). Therefore, estimates of species such as grebes are almost certainly under-estimated. In the context of the WBPHS, the count statistic is the number of individuals of a particular species observed at a particular wetland. The relationship between the expected count statistic ($E(C_i)$) and the state variable can be expressed as:

$$E(C_i) = N_i p_i, \tag{2.1}$$

where $N_i$ the true abundance, and $p_i$ the probability of detection (Lancia et al. 1994). To obtain estimates of true abundance, I estimated the probability of detection which, in this case, is obtained by including supplementary information gained through use of a repeated counts method. Thus,

$$\hat{N}_i = \frac{C_i}{\hat{p}_i}. \quad (2.2)$$

In the context of biological hypotheses and monitoring programs, research typically focuses on ecological state processes (e.g., abundance) while detection probability is considered a nuisance parameter that is required for obtaining unbiased estimates. For the purposes of this chapter, however, the detection probability of WBPHS ground crews is the primary parameter of interest.

## 2.2 Methods

### 2.2.1 Data collection

I collected supplemental data on abundance of grebes during the WBPHS using two methods to estimate species-specific and survey-specific detection probabilities between 9-24 May 2010 and 9-27 May 2011. Survey segments were located in the prairie and parkland ecoregions within south-central Saskatchewan.

### 2.2.2 Survey protocol

I developed a survey protocol designed specifically for detecting horned and pied-billed grebes during a 4 min call-broadcast survey (hereafter grebe protocol; Appendix A). Pied-billed grebes often occupy areas with extensive cover (Faaborg 1976) and detection increases (both visual and aural) with the use of call broadcasts for both conspecifics and heterospecifics when compared with passive surveys (Gibbs and Melvin 1993, Erwin et al. 2002, Conway and Gibbs 2005, Conway and Nadeau 2010). By using a protocol that broadcasts the calls of the subordinate species first (i.e., horned grebes; Osnas 2003), I expected detection to increase for horned grebes where they are present. The sequence of calls based on order of dominance should also increase detection on wetlands where pied-billed grebes are present, i.e., because pied-billed grebes are known to displace horned grebes and are thus the dominant species.

I trained all observers on the survey protocol and habitat assessment methods through demonstration until they were proficient with the protocol. All surveys were conducted during periods of good weather conditions, and surveys were not conducted when precipitation exceeded a light drizzle or wind exceeded 38 kph (Beaufort scale = 5). Ambient temperature, precipitation, wind speed, and percentage cloud cover were recorded at the start of each survey. Temperature was measured using a thermometer (nearest 1 degree Celsius), wind speed using the Beaufort scale (ranging from 0 [0 kph] to 5 [39 kph]), and precipitation (yes, no) and cloud cover (nearest 10%, range 0-100%) were estimated by the observers.

Red-necked (*Podiceps grisegena*) and eared (*Podiceps nigricollis*) grebe counts were also documented but were not included in analyses because of low sample sizes. For example, red-necked grebes are a boreal species and are not typically found within the study area and eared grebes are colonial nesters that were rarely found within study sites.

### 2.2.3 Repeated counts models

Repeated counts models provide a two-stage hierarchical modeling framework to simultaneously estimate abundance and detection probability for spatially replicated counts (Royle 2004). The repeated counts, two counts in this case of this study, provide an encounter history for each site (i.e., wetland) that is then incorporated into a binomial-Poisson mixture modeling framework (Royle 2004). For example, a wetland with an encounter history of '0,2' describes a sampling situation where no individuals were detected during the first count and two individuals were detected during the second count. This method does not require reconciliation of data between surveys and thus does not require the identification of individuals.

Here, I conduct repeated counts on a subset of wetlands on WBPHS ground segments at two temporal scales where the first count represents the WBPHS ground crew count and the

second count represents a count using the grebe protocol. Because the repeated counts use a different survey protocol, I model this difference as a covariate that provides a detection probability estimate for both the WBPHS protocol and the grebe protocol. The two temporal scales were: 1) a same day repeated count (SDRC) where the WBPHS count was immediately followed by the grebe protocol count, and; 2) a different day repeated count (DDRC) where the WBPHS count was followed by the grebe protocol count 24-48 hours later.

2.2.3.1 Same day repeated count (SDRC)

Subsets of wetlands on each of 34 WBPHS ground segments in Saskatchewan (Fig. 2.3) were surveyed using the SDRC where the WBPHS protocol (count 1) was immediately followed by the call-broadcast grebe protocol (count 2). I selected a stratified random sample of wetlands (n = 10-12) per survey segment based on wetland permanency that included seasonal, semi-permanent, permanent, and artificial wetlands (Table 2.1; U.S. Fish and Wildlife Service and Canadian Wildlife Service1987; Shaw and Fredline 1956; Stewart and Kantrud 1971). Wetland permanency was identified using WBPHS habitat data collected the previous year. If a wetland was unavailable for survey (e.g., dry or destroyed by drainage), the closest available wetland of the same permanency class was used. On occasion, not all wetlands or segments were completed due to logistical constraints.

For each wetland, ground crew members conducted the WBPHS protocol by counting all waterfowl and grebe species and then immediately conducted the grebe protocol from the best possible vantage point. To maintain independence between counts, grebe detections in count 2 are only documented when an individual is seen or heard during that new time period; thus, there should be no influence of prior detections from count 1. The grebe protocol (an active call-

broadcast survey) was always conducted after the WBPHS (passive survey) to circumvent influencing the detection probability of the WBPHS.

Ground crews in Saskatchewan typically conduct a "beat-out" on wetlands with abundant emergent vegetation to flush any remaining hidden waterfowl. This was not conducted until after the repeated counts to avoid disturbing grebes, and thus reducing detection probabilities, nor was any grebe detection during the beat-out included in the repeated counts analysis.

2.2.3.2 Different day repeated count (DDRC)

A subset of wetlands on a subset of WBPHS ground segments (n = 6 and 7 segments in 2010 and 2011, respectively; Fig. 3.1) were resurveyed using the grebe protocol by a two-person "shadow crew", between 24-48 hr (weather dependent) after the WBPHS ground crew survey. This was designed to provide additional information on species-specific and survey-specific detection probabilities while using the WBPHS and grebe protocols. In this repeated counts sampling scenario, the WBPHS is considered count 1 and the shadow crew is count 2.

Using historic grebe count data from the WBHPS, I selected a subset of ground segments based on a stratified random sample of survey segments with relatively high and low grebe abundances (5.8-11.6 $km^2$; Fig. 3.1), as was required to meet objectives described in Chapter 3. Only sites within 200 km of Saskatoon, SK, were considered due to logistical constraints. The shadow crew resurveyed all wetlands that received the SDRC method, plus an additional stratified random sample of wetlands to increase sample sizes (n = 17-45, varying by segment).

One drawback of using the DDRC is that weather conditions between survey days may change drastically. In one instance, the WBPHS identified many grebes during the first count on one segment, but 24 hr later there was strong wind and no grebes were detected by the shadow

crew. To reduce this bias, I removed this specific segment from analyses. I also examined the field data for reports of any other such instances and found no obvious anomalies.

2.2.3.3 WBPHS detection probability

Detection probabilities estimated using the SDRC approach suggest that detection probability using the grebe protocol is 1.0 (Table 2.2). In reality, observers are rarely capable of detecting all individuals during any survey (McKenzie et al. 2002; 2006) even when an active call-broadcast protocol is used. Thus, WBPHS detection probabilities estimated using the SDRC should be biased low. To explore this potential bias, I used data obtained from repeated surveys of many wetlands (112 and 115 wetlands in 2010 and 2011, respectively) revisited three times during the breeding season (i.e., to identify factors related to grebe habitat selection; see Chapter 3). For the purposes of this chapter, I analyzed three visits as repeated counts of abundance to derive detection probability estimates that allowed me to estimate species-specific detection probabilities using the grebe protocol which can then be used to adjust WBPHS detection probabilities.

The realized detection probability of the WBPHS ( $\hat{p}^{r}$) was calculated as the product of the WBPHS ( $\hat{p}^{a}$) detection probability and the grebe protocol ( $\hat{p}^{gp}$) detection probability that was obtained from repeat visits. This assumes that the $\hat{p}^{gp}$ does not vary between the WBPHS and the revisits outlined in Chapter 3. The variance is estimated using the *Delta Method*.

**2.2.4 Data analysis**

The statistical program R (R Development Core Team 2011) and the 'pcount' function (which fits binomial-Poisson mixture models in the 'unmarked' package; Fiske and Chandler 2011) were used to build models to estimate species-specific and survey-specific detection probabilities (Royle 2004). For the SDRC and DDRC analyses, I considered how detection

probability could be influenced by ambient temperature, precipitation, wind speed, and percentage cloud cover. However, due to the sparse data and relatively small sample sizes, only observer differences were considered in the final analyses because the increased number of estimable parameters resulted in poor precision of estimates.

The three repeat visits (data from Chapter 3) were analyzed using the same binomial-Poisson mixture model described above. I elected to analyze the data in two stages, modeling detection probability first, followed by including covariates influencing the abundance estimation. I considered that detection probability could be influenced by ambient temperature, precipitation, wind speed, percentage cloud cover, wetland area, the ratio of emergent vegetation to open water, and visit number (to look for temporal change) while maintaining constant occupancy probability. I used an information theoretic approach (Burnham and Anderson 2002) and for each candidate set (each species and year) I did not include any variable for final analyzes whose cumulative model weight (summed Akaike weights across all the models in the set where a particular variable occurs; Burnham and Anderson 2002) was $\leq 0.65$. As a result, horned grebes in 2010 and 2011 were modeled with constant detection probability while pied-billed grebes in 2010 and 2011 were modeled with an effect of wetland area. Model selection procedures suggested no support for a temporal change in detection probability between the three visits. Due to model selection uncertainty, final parameter estimates were obtained using model averaging that included all models in each candidate set (Burnham and Anderson 2002).

## 2.3 Results

### 2.3.1 Same day repeated count (SDRC)

Totals of 145 and 208 wetlands were surveyed using the SDRC method in 2010 and 2011, respectively. Uncorrected counts of grebes obtained via the WBPHS varied considerably between species and years (Fig. 2.4). WBPHS protocol detection probabilities for horned grebes did not differ between 2010 and 2011 and averaged 0.743 (Table 2.2). Pied-billed grebe detection probabilities, however, showed greater annual variation and averaged 0.360 in 2010 and 2011 (Table 2.2). Detection probabilities using the grebe protocol for horned grebes approached 1.0 in all cases (Table 2.2). These results suggest that grebes detected by the WBPHS protocol (count 1) were almost always subsequently detected by the grebe protocol (count 2; i.e., $\hat{p}^{b} = 1$).

### 2.3.2 Different day repeated count (DDRC)

The DDRC method used to determine species-specific and survey-specific detection probabilities did not perform as well as the SDRC method. Estimates for the WBPHS and shadow crew surveys had greater variation and poorer precision (Table 2.3) when compared to SDRC estimates (Table 2.2). Because the same protocol was used during the WBPHS and by the shadow crew, I expected detection probabilities to be similar, but they were not. These results suggest that methodological pit-falls produce poor estimates when re-surveying wetlands 24-48 hr after the WBPHS ground crews (e.g., failing to meet the assumption of closure with no immigration or emigration).

### 2.3.2 WBPHS detection probability

The WBPHS detection probabilities are approximately 22-27% lower for horned grebes (average 0.478, 2010 and 2011) and approximately 15-22% lower for pied-billed grebes (average

0.177, 2010 and 2011) when compared to estimates derived from the SDRC method (Table 2.2; Fig. 2.4).

## 2.4 Discussion

Detection probabilities were higher when using a survey that included a call-broadcast protocol for grebes than when a passive survey was used. The performance of both repeated count methods varied considerably with regard to their estimates, precision, and logistical and practical efficiencies. Of the two methods used to determine species-specific and survey-specific detection probabilities of grebes, the SDRC provides the most precise estimates and is logistically simpler. Conducting additional surveys 24-48 hr after the WBPHS ground crew (i.e., DDRC) presented several noticeable disadvantages. First, weather variability between days (although not modeled in final analyses due to small sample sizes) can likely significantly alter detection probabilities. Second, Ferguson and Sealy (1983) showed that horned grebes in southern Manitoba established territories as early as 7 May and continued throughout the month of May. Thus, it is possible that birds may not be available during both time periods as a result of ongoing territory selection (i.e., local movements among wetlands), violating the assumption of closure. Finally, observer inexperience also appeared to contribute to poor estimates, particularly in 2011, and providing additional observers for future efforts may not be logistically or financially possible.

Aside from providing less biased estimates, conducting the repeated counts method on a subset of wetlands during the WBPHS (SDRC) circumvents the pit-falls described above and is logistically and financially superior. For example, the SDRC requires that a single observer collect supplementary data on a wetland already being surveyed; the additional time requirement is approximately four min per wetland (or 40 min per segment assuming a subset of 10

wetlands). A greater number of wetlands was surveyed in 2011 than in 2010 due to greater experience and familiarity with the additional work. Because the grebe protocol is conducted immediately after the WBPHS count, the assumption of closure is maintained.

As expected, the detection probability by WBPHS ground crew members for pied-billed grebes was lower than that for horned grebes. Estimates are greatly improved with the use of a call-broadcast protocol and detection probabilities of up to 0.67 are attainable. However, I believe that the low rate at which WBPHS ground crews detect pied-billed grebes does not provide support for continuing their inclusion in future monitoring programs. For example, in 2010, WBPHS ground crews observed a total of 25 individual pied-billed grebes on all 34 Saskatchewan segments combined. Assuming a realized detection probability of 0.248, the relative abundance would be approximately 101 individuals. From analyses in Chapter 3, pied-billed grebe occupancy probability in 2010 was 0.155 ± 0.039 (SE). Considering that one of the survey segments (*Hanley*) had 115 semi-permanent and permanent wetlands in 2010, approximately 18 occupied wetlands were on that segment. Assuming a single pair per occupied wetland, the estimated abundance for this segment is 36 individuals, exceeding the provincial total count (25) obtained during the WBPHS. I attribute this to the low rate at which WBPHS ground crews detect pied-billed grebes which do not allow for reliable estimates, and thus inferring variation in annual breeding populations from these data should not be considered.

On the other hand, horned grebes were detected at a higher rate during the WBPHS ground surveys, presumably due to their less secretive behaviours. Annual variation in detection probability did not occur for horned grebes plus the average detection probability in 2010 and 2011 of 0.478 which may merit the inclusion of this species in ongoing monitoring.

### 2.4.1 Management recommendations

*Pied-billed grebes*: Results of this investigation suggest that pied-billed grebe monitoring cannot be efficiently implemented into the current WBPHS ground crew survey protocol without significantly increasing the number of wetlands that are surveyed using a protocol designed specifically for this species. This study used stratified random sampling to select seasonal, semi-permanent, permanent, and occasionally artificial wetlands for estimation of wetland occupancy by grebes; in future, I would suggest not considering seasonal wetlands because there are rarely used by grebes (Chapter 3). Although this would increase the number of suitable habitats surveyed by ground crews using the grebe protocol, it is still likely that the sample size would be too small to effectively monitor annual or spatial variation in pied-billed grebe populations. The low rates of detection present serious implications for detecting population trends. Conservation initiatives concerned with the population status and trend of pied-billed grebes should consider other means of monitoring such as Bird Studies Canada's Prairie and Parkland Marsh Monitoring Program (Bird Studies Canada 2012) and focus on obtaining reliable abundance estimates while accounting for detection.

*Horned grebes*: Because the detection probabilities of horned grebes on the WBPHS ground crew surveys are consistently high, the relative abundance may be used as a population index to monitor annual and spatial variation in abundances provided that all grebe observations are recorded. Although the raw annual counts may be used themselves as an index, I suggest including the grebe protocol on a subset of semi-permanent and permanent wetlands (n = 10) on all segments so that annual detection probabilities (e.g., that could vary due to yearly habitat changes) can be estimated without significantly increasing survey effort. Even a single survey using an active call-broadcast method has imperfect detection and that not accounting for

realized detection probabilities will result in abundance estimates being biased low. Additionally, expanding these methods to include Alberta and Manitoba WBPHS ground crew areas would provide broader-scale monitoring of grebe distributions and relative abundances over time. Furthermore, because the WBPHS ground segments are centered on roads, examining whether or not grebe breeding densities vary in relation to roads should be a priority because wetland densities and species-specific wetland use along roads may not be representative of the larger landscape. For example, Austin et al. (2000) found that wetland densities were greater in 400 m wide transects (same width as the WBPHS) when compared to 800 m wide transects. Additionally, a wetland area bias occurred where smaller (0.08-1.6 ha) semi-permanent and permanent wetlands were over-represented in the 400 m wide transect and larger (>11 ha) wetlands were under-represented in both the 400 m and 800 m wide transects. Austin et al.'s results showed that some species were more likely to occur on the 400 m wide transect, while others were more likely to occur in the 800 m wide transect. For grebes, this may indicate that abundance estimates are higher on the WBPHS ground segments and extrapolating these densities to the larger landscape could be problematic.

Including horned grebes in the WBPHS ground crew surveys would improve population estimates for a Species of Special Concern (COSEWIC 2009). Few existing monitoring programs for at-risk species have the broad-scale monitoring potential that the WBPHS ground component could provide for horned grebes, and with little additional effort. The primary expenses for any avian monitoring program are those associated with logistics of collecting data across vast expanses of habitat (e.g., wages, transportation, and accommodations). Because the WBPHS ground component is a pre-existing large-scale operation, inclusion of horned grebes may be financially and logistically simple compared to alternative methods. Although providing

long term population status and trend information is valuable, it rarely provides insight into reasons for population declines. Therefore, management programs must also consider smaller scale research initiatives that identify high quality habitat(s) and monitor these critical habitats over time.

## 2.5 Tables

Table 2.1 - Summary of the wetland classification criteria used in this study and by the WBPHS.

| Class | Explanation |
|---|---|
| Type 1 | *Temporary*: persists < 3 weeks (depth < 6 in) |
| Type 3 | *Seasonal*: persists > 3 weeks, usually dry by early July (depth > 6 in) |
| Type 4 | *Semi-permanent*: persists into autumn 7 out of 10 years (depth > 6 in) |
| Type 5 | *Permanent*: deep marshes and lakes where water persists throughout the year except during periods of extreme drought (depth > 6 in) |

Table 2.2 - Summary of detection probabilities using the Same Day Repeated Count (SDRC) method and realized detection probability of the WBPHS protocol, 2010 and 2011, Saskatchewan. Also see Fig. 2.2.

| Species | Year | $\hat{p}^{a}$ | $(\hat{SE}^{a})$ | $\hat{p}^{b}$ | $(\hat{SE}^{b})$ | $\hat{p}^{gp}$ | $(\hat{SE}^{gp})$ | $\hat{p}^{r}$ | $(\hat{SE}^{r})$ |
|---|---|---|---|---|---|---|---|---|---|
| HOGR | 2010 | 0.774 | 0.075 | 1.000 | 0.005 | 0.670 | 0.044 | 0.518 | 0.061 |
| HOGR | 2011 | 0.711 | 0.049 | 0.957 | 0.042 | 0.614 | 0.048 | 0.437 | 0.046 |
| PBGR | 2010 | 0.470 | 0.121 | 1.000 | 0.004 | 0.528 | 0.095 | 0.248 | 0.079 |
| PBGR | 2011 | 0.250 | 0.088 | 1.000 | 0.002 | 0.418 | 0.121 | 0.105 | 0.049 |

[a] probability of detection and associated standard error of count 1 (WBPHS protocol)

[b] probability of detection and associated standard error of count 2 (grebe protocol)

[gp] probability of detection and associated standard error of using the grebe protocol (as estimated based on repeated visits to wetlands after the WBPHS).

[r] realized detection probability of count 1 ($\hat{p}^{a} * \hat{p}^{gp}$)

Table 2.3 - Summary of detection probabilities using the Different Day Repeated Count (DDRC) method that includes the WBPHS and shadow crew surveys.

| Species | Year | $\hat{p}^{a}$ | $\hat{SE}^{a}$ | $\hat{p}^{sc}$ | $\hat{SE}^{sc}$ |
|---|---|---|---|---|---|
| HOGR | 2010 | 0.692 | 0.107 | 0.423 | 0.086 |
| HOGR | 2011 | 0.326 | 0.095 | 0.571 | 0.139 |
| PBGR | 2010 | 0.333 | 0.192 | 0.999 | 0.010 |
| PBGR | 2011 | 0.003 | 0.007 | 0.027 | 0.054 |

[a] probability of detection and associated standard error of count 1 (WBPHS protocol)

[sc] probability of detection and associated standard error of count 2 (shadow crew)

## 2.6 Figures

**Figure 2.1** – Survey strata (numbers contained in circles) and transects (horizontal lines within strata) of the Waterfowl Breeding Population and Habitat Survey. Unfilled strata represent the traditional survey area and grey strata represent the eastern survey area (U.S. Fish and Wildlife Service 2011).

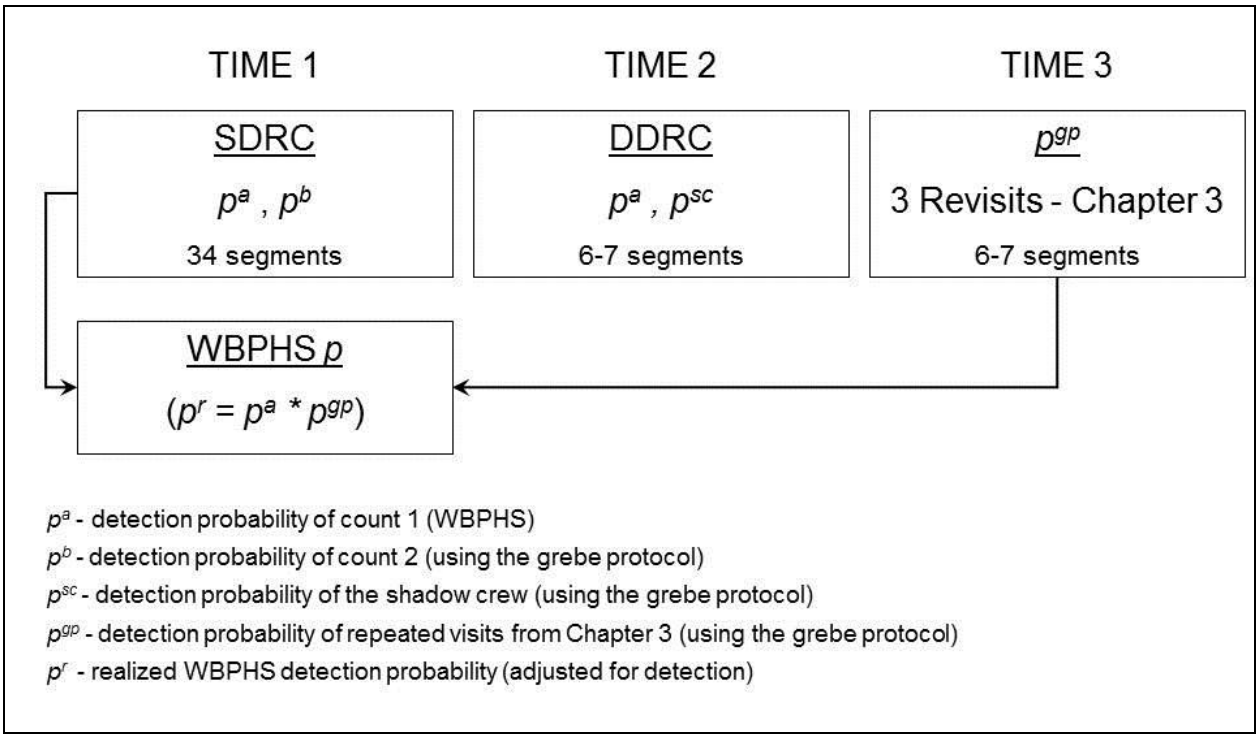


**Figure 2.2** - Diagram of the survey components including the same day repeated count method (SDRC; see section 2.2.3.1) and the different day repeated count method (DDRC; see section 2.2.3.2) and associated detection probabilities (*p*).

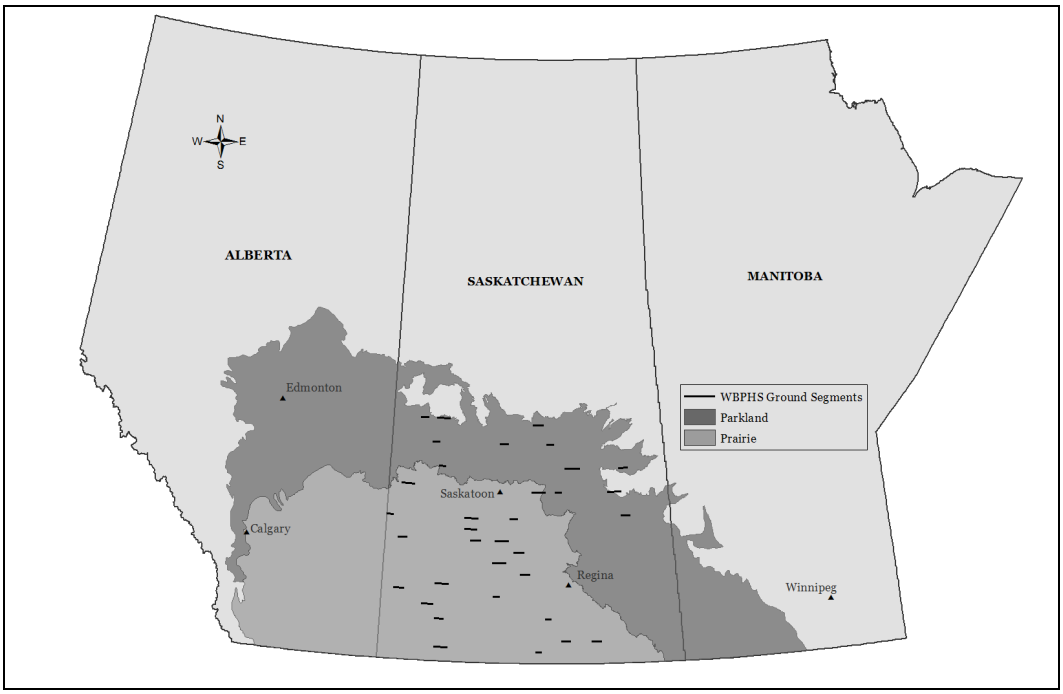


**Figure 2.3** - Study sites within Saskatchewan, Canadian Prairie Pothole Region. Also shown are the prairie and parkland ecoregions.

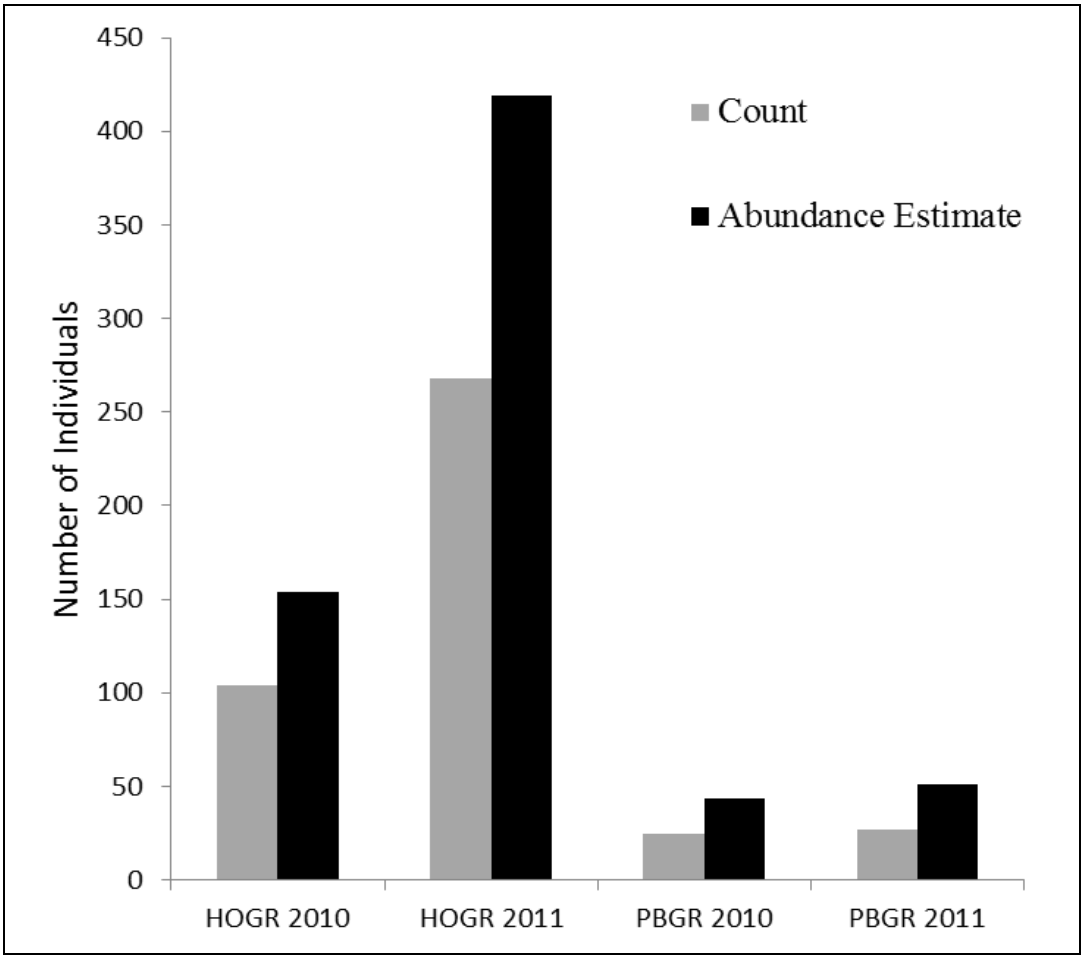


**Figure 2.4** - WBPHS ground crew counts compared to abundance estimates of horned (HOGR) and pied-billed (PBGR) grebes in 2010 and 2011.

# CHAPTER 3. HABITAT OCCUPANCY AND DISTRIBUTION OF GREBES IN PRAIRIE CANADA

## 3.1 Introduction

The Prairie Pothole Region (PPR) of North America is characterized by millions of post-glacial depressions that have created a dynamic wetland ecosystem that contains a disproportionately high level of biodiversity (Zedler and Kercher 2005; Dudgeon 2006). The PPR is particularly important for 10 species of waterfowl, 22 species of landbirds, 12 species of shorebirds, and 29 species of waterbirds (e.g., bitterns (family Ardeidae), gulls (family Laridae), terns (family Sternidae), rails (family Rallidae), and grebes (family Podiceps)) that regularly breed there (Prairie Habitat Joint Venture 2008). Of these groups of birds, research has focused primarily on the breeding and production of waterfowl species due to their high economic value, associated with hunting. Knowledge about the breeding biology of waterbirds is more limited, yet understanding processes that affect distribution patterns and productivity could provide insights into actions needed to achieve conservation goals. Furthermore, waterbird research has focused primarily on breeding habitat use or selection but has seldom examined how productivity is related to characteristics of wetlands used by breeding birds. Determining habitat associations and productivity relationships for species of conservation concern is vital for development of habitat management programs or policy initiatives.

Here, I identify the breeding and brood-rearing habitats used by two species of waterbirds, horned (*Podiceps auritus*) and pied-billed (*Podilymbus podiceps*) grebes, in the prairie and parkland ecoregions of Saskatchewan, and examine patterns of habitat selection at varying spatial scales. Presumably, adult grebes settle at higher densities in areas of higher overall productivity, so I also tested whether grebe breeding densities are indicative of more

productive areas as indexed by brood abundance. Finally, I consider the influence of interspecific competition among grebe species on breeding habitat use, as suggested previously by Faaborg (1976) and Osnas (2005), while accounting for imperfect detection.

### 3.1.1 Habitat selection

Habitat selection theory predicts that animals should prefer habitats where individuals can realize higher survival and reproductive rates (Levins 1968; Fretwell and Lucas 1970). Identifying the factors and processes that influence patterns of habitat selection is a central goal of ecology (Krebs 1994). Habitat selection is a hierarchical process in which factors affect an individual animal's decisions across regional, landscape, macrohabitat, and microhabitat scales (e.g., Johnson 1980, Saab 1999, Deppe and Rotenberry 2008). Strong relationships have been reported between physical attributes of wetland habitats and occupancy in birds and other taxa. For example, wetland area is considered one of the most important characteristics in predicting marshbird species occurrences and abundances (aside from simply providing more area for more individuals, there may be increased resources available; Brown and Dinsmore 1986; Naugle et al. 1999). More recently, there has been an increasing emphasis on processes that operate at broader spatial scales (Naugle et al. 1999, 2000; Fairbairn and Dinsmore 2001; Tozer et al. 2010). In many cases, resources are distributed unevenly as opposed to uniformly or randomly (Ettema and Wardle 2002). Thus, the distribution and habitat use of a species is also expected to vary with landscape heterogeneity, and the factors and processes involved in habitat selection likely also operate at varying spatial scales.

There is limited information about breeding habitat selection and productivity of grebe species (family Podicipedidae). Wetland occupancy by horned and pied-billed grebes is positively correlated with wetland size, depth, and amount of vegetated area (Osnas 2003).

Similarly, Naugle et al. (1999) showed that pied-billed grebes select breeding sites based solely on between-patch variation, not landscape composition. No studies have considered effects of landscape-level effects on habitat use by horned grebes. Furthermore, studies simultaneously examining habitat use by breeding waterbirds and subsequent reproductive success are absent (Tozer et al. 2010). In this study, I estimated wetland occupancy by breeding and brood-rearing horned and pied-billed grebes and evaluated occupancy probability relative to wetland and landscape characteristics.

Because higher densities of breeding individuals may reflect more available resources and higher reproductive success, breeding densities are often used to infer habitat quality (van Horne 1983). However, density of breeding adults may not always be a reliable indicator of habitat quality (e.g., van Horne 1983; Vickery et al. 2002; Bock and Jones 2004). This disconnect between density and habitat quality, according to van Horne (1983), may develop when the distribution of individuals across habitats within a population follows an ideal despotic distribution pattern. It this case, high quality habitats are occupied by dominant individuals that force subordinate individuals into sub-optimal habitats where fitness is lower (Fretwell and Lucas 1970). Secondly, breeding distributions and densities may be influenced by factors operating at another place or time (van Horn 1983). For example, migratory species' populations may be influenced by factors on the wintering grounds (i.e., a different time and place) that in turn impact distributions of individuals on the breeding grounds. A third condition, offered by Bock and Jones (2004), suggests that this disconnect may develop through an ecological trap. For example, populations that breed in highly altered landscapes may no longer be capable of identifying and selecting habitats that result in the highest reproductive success (Bock and Jones 2004). Horned and pied-billed grebes are highly territorial, migratory species that breed in

wetlands in highly altered heterogeneous landscapes; thus, it may be unwise to assume that breeding densities provide a reliable indicator of habitat quality.

I tested the assumption that grebe productivity (indexed by brood abundance) of each study site is positively related to density of breeding adults. If this assumption is valid, then models developed to portray and predict variation in species-specific occupancy of wetlands by breeding adult grebes could be used to infer variation in productivity.

### 3.1.2 Competition

A putative species-specific hierarchy or sequence of wetland use presumes that pied-billed grebes are the dominant species and evict horned grebes from established territories; this pattern does not function reciprocally (Osnas 2003). Evidence suggests that although horned and pied-billed grebes have overlapping macrohabitat preferences (e.g., area and depth), they have different microhabitat preferences (e.g., vegetation interspersion) that may serve to limit interspecific competition between the two species (Nudds 1982). Pied-billed grebes may act despotically, by either occupying or usurping better breeding habitats and then forcing resident horned grebes into sub-optimal habitats where productivity is lower. Understanding this relationship will provide information regarding habitat selection and productivity patterns of grebes, particularly for horned grebes. There will be certain habitats that provide suitable breeding habitat for both species and, thus, I predict that the presence of pied-billed grebes will negatively influence the occupancy probability of horned grebes.

## 3.2 Methods

### 3.2.1 Study site selection

Surveys of grebes and wetlands were conducted on 6 and 7 unique study sites in 2010 and 2011, respectively, in areas of northern prairie and aspen (*Populus tremuloides*) parkland

ecoregions of the PPR. Using historic grebe counts from the Waterfowl Breeding Population and Habitat Survey (WBPHS; an annual continental survey conducted jointly by the United States Fish and Wildlife Service and the Canadian Wildlife Service), I selected study sites based on a random subset of ground segments that had relatively high and low grebe abundances (Fig. 3.1). These survey segments are utilized for ground counts of waterfowl species to provide visibility correction factors for more extensive aerial counts (U.S. Fish and Wildlife Service and Canadian Wildlife Service 1987). Segments range from 13-29 km long and are 400 m wide and centered on a roadway (3.25-7.25 $km^2$); therefore counts are conducted on 200 m on both sides of the road. Only segments within 200 km of Saskatoon, SK, were considered due to logistical constraints. On each segment, 17-45 wetlands were selected based on a stratified random sample of seasonal, semi-permanent, permanent, and artificial wetlands (Chapter 2; Table 2.1).

### 3.2.2 Survey protocols

I developed a survey protocol designed specifically for detecting horned and pied-billed grebes during a 4 min call-broadcast survey (hereafter grebe protocol; Appendix A). Pied-billed grebes often occupy areas with extensive cover (Faaborg 1976) and detection increases with the use of call broadcasts for both conspecifics and heterospecifics when compared with passive surveys (Gibbs and Melvin 1993, Erwin et al. 2002, Conway and Gibbs 2005, Conway and Nadeau 2010). Thus, by using a protocol that broadcasts the calls of the less dominant species first (i.e., horned grebes; Osnas 2003), I expected detection to increase for horned grebes where they are present. The sequence of calls based on order of dominance should also increase detection on wetlands where pied-billed grebes are present, i.e., because pied-billed grebes are known to be dominant over horned grebes.

I trained all observers on the survey protocol and habitat assessment methods through demonstration until they were proficient with the protocol. All surveys were conducted during periods of good weather conditions, and surveys were not conducted when precipitation exceeded a light drizzle or wind exceeded 38 kph (Beaufort scale = 5). Ambient temperature, precipitation, wind speed, wind direction, and percentage cloud cover were recorded at the start of each survey. Temperature was measured using a thermometer (nearest 1 degree Celsius), wind speed using the Beaufort scale (ranging from 0 [0 kph] to 5 [39 kph]), and precipitation (yes, no) and cloud cover (nearest 10%, range 0-100%) were estimated by the observers.

Using handheld GPS units (Garmin GPSMAP 60CSx), track files for measurement of wetland perimeter were created by walking along the water's edge of all wetlands and storing a track point every 1 sec. Track files were then imported into ArcGIS 10 (ESRI 2011) and converted to polygons representing wetland perimeters for calculation of wetland area.

### 3.2.3 Surveys of adult grebes

Three visits to wetlands on each site were conduced between 6-26 June and 27 May-15 June in 2010 and 2011, respectively, at approximately 7 day intervals. Vocalization probability is highest during a 2 hr period following sunrise (Conway and Gibbs 2005; Conway 2009). To increase the number of wetlands surveyed at each site, surveys commenced shortly after sunrise and were typically finished before 10:00 CST.

### 3.2.4 Surveys of grebe broods

Three additional visits to wetlands on each site were conducted between 5 July-16 August and 11-27 July in 2010 and 2011, respectively. The call-broadcast protocol was used although aural response rates typically decline during this period (Conway 2009; Conway and Gibbs 2011). Surveys commenced shortly after sunrise and were usually completed before 10:00

CST to coincide with the period when grebes are most active and more likely to be detected. These data enabled me to calculate brood occupancy probabilities.

### 3.2.5 Habitat and landscape classifications

Habitat data were collected once during the breeding bird surveys and once during brood surveys. Information included a visual estimate of the percentage of habitat types within the basin (open water, emergent vegetation, exposed substrate, or woody vegetation), the percentage and type of dominant emergent vegetation, and percentage of upland cover types within 100 m of the wetland (intensive farming, grasslands/hayland, pasture, or wooded area). Percentages of each habitat type were rounded to the nearest 20% at the time of collection to reduce observer bias. Wetland permanency class (see Chapter 2, Table 2.1) was collected once during the breeding season (because it does not change over time) and water level stage (U.S. Fish and Wildlife Service and Canadian Wildlife Service1987; Shaw and Fredline 1956; Stewart and Kantrud 1971). Data were collected by two trained observers and cross-comparisons of habitat assignments were done to improve consistency.

### 3.2.6 Data management

Preliminary analyses indicated that in 2010 and 2011, only 1 of 116 seasonal wetlands was occupied by a horned grebe and none was occupied by a pied-billed grebe. To ensure that occupancy estimates were not biased by this clear avoidance of seasonal wetlands by both species, I removed all seasonal wetlands from subsequent analyses. Less than 2% of wetlands surveyed in 2010 and 2011 were >4 ha (Figs. 3.2). Because detection probability is low on large wetlands and sample size is small, limiting inferences about these types of wetlands, I excluded 4-12 ha wetlands from analyses.

### 3.2.7 Occupancy estimation

Patterns of habitat occupancy provide measures of how animals are distributed in time and space, so occupancy is fundamentally linked to abundance (MacKenzie et al. 2006). Here, occupancy is the proportion of wetlands within an area occupied by a species at distinct survey times (MacKenzie et al. 2002). Relative to abundance data, occupancy data are more efficient to collect and are well suited for large-scale monitoring programs where the entire survey area is too large to acquire reliable abundance estimates. Thus, it may be sufficient to determine the proportion of habitats occupied by a species in smaller areas and then extrapolate occupancy to larger areas (Royle and Nichols 2003). Although complete count data were recorded during all surveys, counts were collapsed into detection/non-detection data. An encounter history was then created using a sequence of 1s and 0s, with 1 indicating detection and 0 signifying non-detection. For example, an encounter history of "011" represents a situation where a grebe was not detected on the first visit but was detected on the second and third visits to a specific wetland. For territorial species such as grebes, wetlands may typically be occupied by a single breeding pair which provides a good index of abundance. Wetlands seldom had >2 individuals (i.e., one breeding pair; Fig. 3.3).

The following assumptions must be met when using occupancy modeling: 1) the occupancy status of the wetland does not change over the survey season, i.e., sites are "closed" with respect to immigration and emigration, for example; 2) the probability of occupancy is equal across all sites, or differences can be modeled using covariates; 3) the probability of detection given occupancy is equal across all sites and surveys, or is a function of covariates; and 4) the detection of a species and detection histories at each location are independent (MacKenzie et al. 2006). Of these, often the assumption of closure receives the most attention and concern.

For example, breeding grebes arrive on the breeding grounds and establish breeding territories but there is a settlement period when some territory holders may be displaced by other individuals. Because of the known dominance hierarchy between breeding grebe species (Osnas 2003), pied-billed grebes may displace horned grebes during this settlement period. To better meet the closure assumption, for this specific study, breeding surveys were delayed until mid to late May (i.e., no WBPHS data were used [Chapter 2]) to avoid this settlement period (Ferguson and Sealy 1983; Mueller and Storer 1999) and brood surveys were delayed until sufficient time had elapsed to ensure that most broods had hatched. If a newly hatched brood was observed before the end of the last brood survey, the previous brood surveys received a 'NA' in the encounter history so that they contributed no information to the occupancy or detection probabilities (i.e., similar to a missing survey). For example, an encounter history of 'NA-1-1' describes a situation where a wetland was surveyed in all three occasions, but a newly hatched brood was observed on visit two (indicating it could not have been available for detection in visit 1) and the brood was detected again on visit three. The observer had to make a decision about whether the brood was old enough to have been available on the first visits and simply not detected, versus not yet hatched and unavailable for detection. There were a total of 2 such encounter histories in 2010 and 2011.

To obtain unbiased estimates of occupancy probability, detectability must be accounted for because observers are rarely able to detect all individuals or species at each survey occasion (Nichols et al. 2000; MacKenzie et al. 2002; Lancia et al. 2005). Detection probability ($p$), as defined for occupancy estimation, refers to the probability of detecting the presence of a species given that at least one individual is located within the sample unit (Thompson 2004).

To examine whether or not densities of breeding adult grebes reliably indicate reproductive success, I compared the density of breeding adults to the density of broods. Density ($D_i$) was calculated as the occupancy probability ($\psi_i$) of a breeding adult or brood weighted by the total number of semi-permanent, permanent and artificial wetlands ($W_i$) in the study area ($A_i$) at time and location *i*:

$$\hat{D}_i = \frac{\hat{\psi}_i * W_i}{A_i} \tag{3.1}$$

To examine the effect of landscape composition on breeding and brood-rearing grebes, I used WBPHS data to separate sites into landscapes with either a relatively low or high density of semi-permanent, permanent, and artificial wetlands. As a result, 4-5 sites (in 2010 and 2011 respectively) had a relatively low wetland density (≤20 wetlands/mi$^2$) and 2 sites had a relatively high wetland density (≥50 wetlands/mi$^2$). Landscape class, corresponding to low or high wetland density, was included as a binary covariate. Finally, to determine whether the presence of one grebe species was associated with the absence of the other species, I included a binary covariate in analyses where a '1' indicated naïve occupancy (if a grebe of species *i* was ever detected on a wetland it was considered "occupied") of the heterospecific species and a 0 indicated absence (MacKenzie et al. 2002; 2006).

### 3.2.8 Data analysis

Using the statistical analysis program R (R Development Core Team 2011) and the R package 'unmarked' (Fiske and Chandler 2011), I built a single-season occupancy model (MacKenzie et al. 2002, 2006) to examine hypothesized effects of competition, wetland structure, and landscape composition on occurrence and productivity of horned and pied-billed grebes. Several of the same wetlands were surveyed in 2010 and 2011 and a new study site was

added in 2011; therefore, to avoid possible problems of pseudoreplication and annual site changes, data from the two years were analyzed separately.

3.2.8.1 Modelling detection probability (*p*)

I elected to analyze the data in two stages, modeling detection probability first, followed by estimating occupancy probability. I considered that detection probability could be influenced by the ambient temperature, precipitation, wind speed, and percentage cloud cover, survey date, time of survey, wetland area, and the ratio of emergent vegetation to open water. The results of this analysis indicated that in general, breeding adult and brood detection probabilities for horned and pied-billed grebes were best explained by a null model that assumed constant detection probability (Appendix B). In two cases where the variable importance ($\sum$ AIC$w_i$) was $\geq 0.70$, the increase in precision of the occupancy and detection probability estimates did not warrant adding the additional parameter. Therefore, all subsequent models were structured with constant detection probability.

3.2.8.2 Modelling occupancy probability

I developed a biologically defensible set of *a priori* models (Burnham and Anderson 2002) to explain grebe occupancy. I considered habitat variables that reportedly influence habitat selection in grebes including wetland size, amount of emergent vegetation, and the presence/absence of heterospecific species (Faaborg 1976; Sugden 1977; Osnas 2003). I hypothesized that occurrence of grebes may be a non-linear function of the amount of vegetation in a particular wetland and therefore included a quadratic term for amount of vegetation. Specifically, preferred habitats may be those where an approximate "hemi-marsh" condition exits (e.g., a ratio of 50:50 vegetation to open water) as reported for breeding waterfowl (Kaminski and Prince 1981; Murkin et al. 1982; Murkin et al. 1997). I combined the proportion

of emergent vegetation and the proportion of open water into a single variable represented by a ratio of emergent vegetation to open water. I also considered a scenario where an interaction may exist between wetland area and the ratio of emergent vegetation to open water.

Although the variables mentioned above were selected using *a priori* hypotheses and results of previous studies, I explored the possibility that other factors could be important determinants of wetland occupancy by grebes. Although landscape scale factors have been shown to be unimportant in the habitat selection of pied-billed grebes (Naugle et al. 1999), I elected to re-examine their potential influence on grebe occupancy. Therefore, I performed logistic regressions to explore possible effects of additional basin habitats (exposed substrate and woody vegetation), dominant vegetation types (cattail (*typha spp.*), sedge (family *Cyperaceae*), rush (*Juncus spp.*), and various grass species), and upland cover (croplands, grasslands/haylands, grazed pasture, and wooded areas) in relation to naïve occupancy (not adjusted for detection). In each case, I concluded that the null model with constant occupancy probability was superior and was consistent with *a priori* expectations, suggesting that these variables could be excluded from future analyses (Burnham and Anderson 2002). Furthermore, while modeling occupancy probability, I included each of the basin habitat, vegetation type, and upland cover covariates mentioned above, in the top model for each candidate set and found that the original top model remained better, thus supporting my decision to remove these covariates from further analyses.

Final analyses included: wetland area (AREA), emergent to open water ratio (EVOW), the naïve occupancy of other species (HTSP; Table 3.1), and landscape (LAND; binary: either relatively low or high wetland density landscapes. Landscapes were clearly distinguished by differences in wetland density (low, <25 semi-permanent and permanent wetlands/ $km^2$; high, >40 semi-permanent and permanent wetlands/ $km^2$). In all cases, I modeled the emergent

vegetation to open water ratio with and without a quadratic term to test whether or not a non-linear relationship existed. In cases where a linear relationship had greater support (based on Akaike's information criterion (AIC) and cumulative variable weights), I excluded the quadratic term from the final candidate sets. For example, breeding horned grebes in 2010 exhibited a linear relationship between occupancy probability and the emergent vegetation to open water ratio, therefore, the final candidate set only included the EVOW term and not the $EVOW^2$ term. Breeding horned grebes in 2011, on the other hand, showed a non-linear relationship and the final candidate set included $EVOW+EVOW^2$ instead of only EVOW. I also considered a multiplicative relationship between wetland area and emergent vegetation in all candidate sets but it was only supported for pied-billed grebe broods in 2011 so was subsequently removed from all other candidate sets. Candidate model sets containing all terms and additive and multiplicative interactions can be found in Appendix C.

Most candidate model sets exhibited model selection uncertainty so model averaging was used for parameter estimation (Burnham and Anderson 2002). Model averaging included all models within the candidate set (instead of only including those within a predetermined $\Delta$AIC) because even poorly supported models contain some information, but their influence on the final parameter estimates are proportional to their AIC weights (Burnham and Anderson 2002).

## 3.3 Results

Totals of 112 and 115 semi-permanent, permanent, and artificial wetlands were surveyed for horned and pied-billed grebes in 2010 and 2011, respectively. Occupancy probability for breeding adult horned and pied-billed grebes, which varied by species, did not differ between years for each species (Table 3.2). However, brood occupancy probabilities for horned grebes

had greater inter-annual variation. Detection probabilities varied widely and are given in Table 3.2.

### 3.3.1 Wetland-specific variables

Amounts of emergent vegetation and open water predicted occupancy probability of horned grebe breeding adults and broods (Tables 3.3-3.6, Figs. 3.4-3.7). Breeding horned grebes and broods had higher predicted occupancy probability in more open wetland habitats with <20% emergent vegetation to open water. With the exception of broods in 2010, this variable was found in all top models (Tables 3.3-3.6) and had cumulative model weight (sum of AIC weights for all models containing a particular variable; $\sum AICw_i$) ranging from 0.609-1.0. On the other hand, pied-billed grebes preferred wetland habitats with approximately 20-40% emergent vegetation. This relationship was evident in 2011 only (Tables 3.8 and 3.10; Figs. 3.8-3.11), with $\sum AICw_i = 0.814$ for breeding adults and 0.910 for broods.

Wetland area was an important variable in predicting the occupancy probability of breeding adults and broods for pied-billed grebes, but not for horned grebes (Table 3.11, Figs. 3.4-3.11). The wetland area term appeared in all top models for breeding adult pied-billed grebes and broods in 2010 and 2011 with $\sum AICw_i$ ranging from 0.572-0.999 (Tables 3.7-3.10).

### 3.3.2 Landscape effects

The density of semi-permanent and permanent wetlands was an important predictor of occupancy probability of breeding adults and broods for both horned and pied-billed grebes (Table 3.11, Figs. 3.4-3.11). Although this variable was found in the top model of all candidate model sets for breeding adults ($\sum AICw_i = 0.509$-$0.841$), it was found to be more influential in all candidate model sets for broods ($\sum AICw_i = 0.613$-$0.937$). In general, there was a positive relationship between a density of semi-permanent, permanent, and artificial wetlands and habitat

use by breeding adult grebes and broods (Figs. 3.4-3.11). Exceptions were breeding adult horned grebes and broods in 2011 (Figs. 3.5 and 3.7).

Although I was unable to examine the reproductive success of individuals or specific breeding pairs in relation to varying landscape conditions, results suggest that there is no discernible difference in the per pair production between low and high wetland density landscapes, as indexed by brood count (Figs. 3.12-3.13). However, high wetland density landscapes typically showed higher overall production of broods, as indexed by brood occupancy.

### 3.3.3 Occupancy of breeding adults and broods

Density of broods was positively correlated with density of breeding adults in both grebe species ($r^2 = 0.81$ and $r^2 = 0.67$ for horned and pied-billed grebes, respectively, with pooled 2010 and 2011 data; Figs. 3.14 and 3.15). Linear regression detected no difference from a slope = 1.0 in the relationship between densities of broods and breeding adults for horned ($\beta = 0.946 \pm 0.139$ (SE), $P = 0.70$) and pied-billed ($\beta = 1.394 \pm 0.293$ (SE), $P = 0.21$) grebes. This suggests that the density of breeding adult grebes is a good predictor of brood density at the scale of the study site.

### 3.3.4 Competition

For horned grebes, the presence of a pied-billed grebe was a strong predictor of breeding and brood occupancy probability (negative association) and was included in the top model in all cases except for broods in 2011 (Tables 3.3-3.6; Figs. 3.4-3.7). When an effect was found (variable contained in a model with <2 ΔAIC; Burnham and Anderson 2002), cumulative model weights for each candidate set also supported this inference ($\sum AICw_i = 0.643\text{-}0.909$). For breeding pied-billed grebes, the presence of a horned grebe was found in the top model (Tables 3.7-3.10) but support was weaker, with $\sum AICw_i = 0.557$; pied-billed grebe occupancy probability

was more strongly influenced by wetland area. The absence of horned grebes proved to be a better predictor for pied-billed grebe brood occupancy probability in 2010 $\sum AICw_i$ =0.845 and was not influential in 2011 (Table 3.11).

Analysis based on naïve occupancy indicated that 3 of 112 (2010) and 2 of 115 (2011) wetlands contained both species of breeding adults and the same wetlands were used by both species during brood-rearing. Additionally, no single wetland, in 2010 and 2011, ever had more than one breeding pair of pied-billed grebes or multiple broods. Horned grebes, however, are more tolerant of conspecifics in some cases (Stedman 2000) and six wetlands were occupied by more than one breeding pair over the duration of the study and in only one case was there more than one brood on a single wetland. Red-necked grebes were present on 12 wetlands in both 2010 and 2011 and were not included in habitat analyses due to small sample sizes. Also, red-necked grebes did not occur evenly across the study area; rather, they occurred in the northern extents of the aspen parkland ecoregion, as anticipated, because they breed predominantly in boreal forest wetlands (Stout and Nuechterlein 1999).

## 3.4 Discussion

My analyses generally support previous studies that have examined the relationship of breeding horned and pied-billed grebe occupancy and wetland-specific habitat characteristics (e.g., Faaborg 1976; 2003), while providing insight into the nonlinearity of some of these relationships. Furthermore, my research explicitly accounted for imperfect detection which was not considered in previous studies so results may be more reliable. In general, breeding horned grebes preferred less densely vegetated wetland habitats and readily occupied wetlands of any size. Breeding pied-billed grebes preferred larger wetlands that were more densely vegetated than those used by horned grebes. Furthermore, I found evidence that breeding horned and pied-

billed grebes do not typically co-occur (Faaborg 1976; Osnas 2003). Although wetland heterogeneity contributes to differential habitat selection and use among grebes, future studies that examine the effects of competition and habitat segregation should consider variation in diet between grebe species as a potential mechanism.

This work has also highlighted the importance of considering the hierarchical processes involved in habitat selection for waterbirds. Because habitat resources are distributed unevenly, we should expect that habitat use and selection follow a similar pattern. Landscape factors have been shown by Naugle et al. (1999) to be inconsequential in determining habitat use patterns in pied-billed grebes. However, my results suggest otherwise. Landscape influenced habitat selection of breeding horned and pied-billed grebes and appeared in the top model for each species and year. Although some results were equivocal, the general trend is that grebes prefer to breed in landscapes with higher wetland densities. This contradicts previous work on pied-billed grebes (Naugle et al. 1999) possibly because of the added reliability of accounting for detection and has never been considered for horned grebes. The exception occurred in 2011 when predicted breeding horned grebe occupancy probability was significantly higher in low wetland density landscapes, possibly due to above-average water conditions that created more available wetland habitat in these landscapes. My results suggest that upland habitat characteristics and land use practices surrounding wetlands (i.e., intensive farming, hay or grasslands, pasture lands, or wooded areas) are generally unimportant in predicting occupancy by grebes.

Waterbird habitat selection studies have focused primarily on breeding adults, and have not typically considered how offspring production is related to habitat characteristics. Wetland occupancy by horned grebe broods was positively associated with the ratio of emergent vegetation in 2011 only, and was not influenced by wetland area. Pied-billed grebe broods, on

the other hand, exhibited greater occupancy probability on larger wetlands with a higher ratio of emergent vegetation to open water. As with breeding adults in 2011, models for broods included a quadratic term and probability of occupancy by broods was lowest on wetlands with no emergent vegetation and those with very little open water. This range of conditions provides dense stands of emergent vegetation for security (e.g., from predators) while maintaining open water areas for foraging.

Grebes select breeding habitats from a continuum of wetland habitats with varying structural qualities (e.g., wetland area or amount of emergent vegetation). Despite the differences in preferred habitats which functions to limit interspecific competition, there are undoubtedly wetlands that provide suitable habitat for both species (Figs. 3.16-3.19). As a result, I expect pied-billed grebes to act as 'despots' on these wetlands, forcing horned grebes into alternate, potentially less productive wetlands.

Source-sink theory predicts that because quality varies among habitats, individuals that secure breeding territories in these high quality areas form the source population which on average allows the population to remain stable or increase, while low quality habitat areas form the sink population that would not persist without the excess production by the source population (Pulliam 1988). Since higher breeding grebe occupancy and overall productivity were prevalent in high wetland density landscapes, breeding grebes may exhibit source-sink population dynamics. Given this, grebe conservation initiatives should focus efforts on maintaining wetland quality in landscapes where grebes breed in higher densities. Further research is needed to determine factors affecting survival (of both adults and offspring) and reproductive success of individuals in varying landscapes, and to better understand the population dynamics of these species. To facilitate this, mark-recapture studies will be needed to closely monitor individuals

which would also provide an opportunity to explore hypotheses of intra- and inter-specific competition.

### 3.4.1 Management implications

Understanding the factors and processes that drive habitat selection and use in breeding and brood-rearing grebes is vital to developing better guidance for habitat conservation programs. Breeding grebes are able to recognize and settle in greater densities in areas of higher overall production and that density is a good indicator of habitat quality despite the potential mechanisms (e.g., ideal despotic distribution, ecological trap, or population limiting factors on the wintering grounds) that can cause this relationship to become decoupled (Van Horne 1983; Bock and Jones 2004). If the density of breeding adults were a misleading indicator of productivity, we would expect that high wetland density landscapes would have significantly reduced densities of broods. I documented a strong positive relationship between the density of breeding adults and the density of broods ($R^2$=0.81 and $R^2$=0.67 for horned and pied-billed grebes, respectively), and obtained no evidence of a decrease in brood density with increasing density of breeding pairs. Although grebes are found in relatively low densities throughout many parts of the prairies (and 5 of 7 sites in this study), high wetland density landscapes have higher densities of breeding adults and higher densities of broods. It becomes very challenging, in terms of time and costs, to continually monitor breeding populations and subsequent reproductive success. Since brood densities are positively related to density of breeding adults, conservation initiatives can develop models used to portray and predict variation in species-specific wetland occupancy by breeding grebes that could also be used to infer variation in productivity.

## Tables 3.5

Table 3.1 - Summary of variables used in model selection procedure for horned and pied-billed grebe occupancy probability ($\psi$) in the Canadian PPR in 2010 and 2011.

| Variable | Explanation |
|---|---|
| AREA | Wetland area in hectares. |
| EVOW | Ratio of the proportion of the basin consisting of emergent vegetation to open water. |
| EVOW2 | A quadratic term for EVOW. |
| HTSP | Presence or absence of the heterospecific species (horned or pied-billed grebes only) |
| LAND | Binary designation of landscapes with a relatively low or high density of semi-permanent and permanent wetlands. |

Table 3.2 - Model-averaged predictions of detection probability ( $\hat{p}$ ) and occupancy probability ( $\hat{\psi}$ ) for breeding adult horned (HOGR) and pied-billed (PBGR) grebes and broods in Saskatchewan, 2010 and 2011.

| Species | Year | $\hat{p}$ | $\hat{p}$ (SÊ) | $\hat{\psi}$ | $\hat{\psi}$ (SÊ) |
|---|---|---|---|---|---|
| *Adults*: | | | | | |
| HOGR | 2010 | 0.78 | 0.04 | 0.30 | 0.05 |
| HOGR | 2011 | 0.83 | 0.04 | 0.29 | 0.08 |
| PBGR | 2010 | 0.70 | 0.07 | 0.16 | 0.04 |
| PBGR | 2011 | 0.44 | 0.09 | 0.23 | 0.09 |
| *Broods*: | | | | | |
| HOGR | 2010 | 0.44 | 0.06 | 0.32 | 0.06 |
| HOGR | 2011 | 0.80 | 0.06 | 0.14 | 0.04 |
| PBGR | 2010 | 0.30 | 0.07 | 0.32 | 0.10 |
| PBGR | 2011 | 0.41 | 0.08 | 0.35 | 0.12 |

Table 3.3 - Summary of the candidate model set ranked by AIC with the best-approximating model at the top for breeding horned grebe occupancy probability (ψ) with constant detection probability *p*(.), Saskatchewan, 2010. Variable names used in models are defined in Table 3.1.

| Model[a] | AIC[a] | ΔAIC[b] | $w_i$[c] | $K$[d] |
|---|---|---|---|---|
| ψ (HTSP+EVOW+LAND) | 246.83 | 0.00 | 0.17 | 5 |
| ψ (HTSP+LAND) | 247.46 | 0.63 | 0.12 | 4 |
| ψ (HTSP+EVOW) | 247.62 | 0.79 | 0.11 | 4 |
| ψ (EVOW+LAND) | 248.49 | 1.66 | 0.07 | 4 |
| ψ (HTSP+AREA+EVOW+LAND) | 248.59 | 1.76 | 0.07 | 6 |
| ψ (EVOW) | 248.59 | 1.77 | 0.07 | 3 |
| ψ (HTSP) | 248.90 | 2.08 | 0.06 | 3 |
| ψ (HTSP+AREA+LAND) | 249.17 | 2.34 | 0.05 | 5 |
| ψ (AREA+EVOW+LAND) | 249.46 | 2.63 | 0.05 | 5 |
| ψ (HTSP+AREA+EVOW) | 249.50 | 2.67 | 0.04 | 5 |
| ψ (LAND) | 249.81 | 2.98 | 0.04 | 3 |
| ψ (AREA+EVOW) | 249.90 | 3.07 | 0.04 | 4 |
| ψ (.) | 250.24 | 3.41 | 0.03 | 2 |
| ψ (AREA+LAND) | 250.59 | 3.76 | 0.03 | 4 |
| ψ (HTSP+AREA) | 250.76 | 3.93 | 0.02 | 4 |
| ψ (AREA) | 251.43 | 4.61 | 0.02 | 3 |

[a] Models are denoted as additive (+); Variables are defined in Table 3.1.

[b] Akaike's Information Criterion.

[c] Difference in AICc relative to smallest value.

[d] Akaike's weight of models.

[e] Number of parameters.

Table 3.4 - Summary of the candidate model set ranked by AIC with the best-approximating model at the top for breeding horned grebe occupancy probability (ψ) with constant detection probability *p*(.), Saskatchewan, 2011. Variable names used in models are defined in Table 3.1.

| Model[a] | AIC[a] | ΔAIC[b] | $w_i$[c] | $K$[d] |
|---|---|---|---|---|
| ψ (HTSP+EVOW+EVOW2+LAND) | 201.70 | 0.00 | 0.46 | 6 |
| ψ (HTSP+AREA+EVOW+EVOW2+LAND) | 202.63 | 0.93 | 0.29 | 7 |
| ψ (HTSP+AREA+EVOW+EVOW2) | 205.06 | 3.36 | 0.09 | 6 |
| ψ (EVOW+EVOW2+LAND) | 205.24 | 3.54 | 0.08 | 5 |
| ψ (HTSP+EVOW+EVOW2) | 205.91 | 4.21 | 0.06 | 5 |
| ψ (AREA+EVOW+EVOW2+LAND) | 207.20 | 5.51 | 0.03 | 6 |
| ψ (EVOW+EVOW2) | 210.95 | 9.25 | 0.00 | 4 |
| ψ (AREA+EVOW+EVOW2) | 212.40 | 10.70 | 0.00 | 5 |
| ψ (HTSP+AREA) | 219.86 | 18.16 | 0.00 | 4 |
| ψ (HTSP+AREA+LAND) | 220.52 | 18.83 | 0.00 | 5 |
| ψ (HTSP+LAND) | 221.30 | 19.60 | 0.00 | 4 |
| ψ (HTSP) | 221.96 | 20.27 | 0.00 | 3 |
| ψ (LAND) | 225.13 | 23.43 | 0.00 | 3 |
| ψ (.) | 226.20 | 24.50 | 0.00 | 2 |
| ψ (AREA+LAND) | 226.59 | 24.90 | 0.00 | 4 |
| ψ (AREA) | 227.03 | 25.34 | 0.00 | 3 |

[a] Models are denoted as additive (+); Variables are defined in Table 3.1.

[b] Akaike's Information Criterion.

[c] Difference in AICc relative to smallest value.

[d] Akaike's weight of models.

[e] Number of parameters.

Table 3.5 - Summary of the candidate model set ranked by AIC with the best-approximating model at the top for horned grebe brood occupancy probability (ψ) with constant detection probability *p*(.), Saskatchewan, 2010. Variable names used in models are defined in Table 3.1.

| Model[a] | AIC[b] | ΔAIC[c] | $w_i$[d] | $K$[e] |
|---|---|---|---|---|
| ψ (HTSP+LAND) | 255.27 | 0.00 | 0.28 | 4 |
| ψ (HTSP+AREA+LAND) | 255.72 | 0.45 | 0.22 | 5 |
| ψ (HTSP+EVOW+LAND) | 257.27 | 2.00 | 0.10 | 5 |
| ψ (HTSP) | 257.51 | 2.24 | 0.09 | 3 |
| ψ (HTSP+AREA+EVOW+LAND) | 257.72 | 2.45 | 0.08 | 6 |
| ψ (HTSP+AREA) | 258.11 | 2.84 | 0.07 | 4 |
| ψ (HTSP+EVOW) | 259.37 | 4.11 | 0.04 | 4 |
| ψ (HTSP+AREA+EVOW) | 259.90 | 4.64 | 0.03 | 5 |
| ψ (AREA+LAND) | 260.63 | 5.37 | 0.02 | 4 |
| ψ (AREA) | 260.95 | 5.68 | 0.02 | 3 |
| ψ (.) | 261.57 | 6.31 | 0.01 | 2 |
| ψ (LAND) | 261.68 | 6.41 | 0.01 | 3 |
| ψ (AREA+EVOW+LAND) | 262.46 | 7.20 | 0.01 | 5 |
| ψ (AREA+EVOW) | 262.56 | 7.29 | 0.01 | 4 |
| ψ (EVOW) | 263.26 | 8.00 | 0.01 | 3 |
| ψ (EVOW+LAND) | 263.53 | 8.26 | 0.00 | 4 |

[a] Models are denoted as additive (+); Variables are defined in Table 3.1.

[b] Akaike's Information Criterion.

[c] Difference in AICc relative to smallest value.

[d] Akaike's weight of models.

[e] Number of parameters.

Table 3.6 - Summary of the candidate model set ranked by AIC with the best-approximating model at the top for horned grebe brood occupancy probability (ψ) with constant detection probability *p*(.), Saskatchewan, 2011. Variable names used in models are defined in Table 3.1.

| Model[a] | AIC[a] | ΔAIC[b] | $w_i$[c] | $K$[d] |
|---|---|---|---|---|
| ψ (EVOW+LAND) | 157.79 | 0.00 | 0.26 | 4 |
| ψ (HTSP+EVOW+LAND) | 158.66 | 0.86 | 0.17 | 5 |
| ψ (HTSP+EVOW) | 159.61 | 1.82 | 0.11 | 4 |
| ψ (EVOW) | 159.67 | 1.88 | 0.10 | 3 |
| ψ (AREA+EVOW+LAND) | 159.76 | 1.96 | 0.10 | 5 |
| ψ (HTSP+AREA+EVOW+LAND) | 160.65 | 2.86 | 0.06 | 6 |
| ψ (HTSP+AREA+EVOW) | 161.32 | 3.53 | 0.05 | 5 |
| ψ (AREA+EVOW) | 161.64 | 3.84 | 0.04 | 4 |
| ψ (LAND) | 162.64 | 4.84 | 0.02 | 3 |
| ψ (.) | 162.72 | 4.93 | 0.02 | 2 |
| ψ (HTSP) | 163.05 | 5.25 | 0.02 | 3 |
| ψ (HTSP+LAND) | 163.49 | 5.70 | 0.02 | 4 |
| ψ (AREA+LAND) | 164.63 | 6.83 | 0.01 | 4 |
| ψ (HTSP+AREA) | 164.67 | 6.87 | 0.01 | 4 |
| ψ (AREA) | 164.68 | 6.88 | 0.01 | 3 |
| ψ (HTSP+AREA+LAND) | 165.42 | 7.62 | 0.01 | 5 |

[a] Models are denoted as additive (+); Variables are defined in Table 3.1.

[b] Akaike's Information Criterion.

[c] Difference in AICc relative to smallest value.

[d] Akaike's weight of models.

[e] Number of parameters.

Table 3.7 - Summary of the candidate model set ranked by AIC with the best-approximating model at the top for breeding pied-billed grebe occupancy probability (ψ) with constant detection probability *p*(.), Saskatchewan, 2010. Variable names used in models are defined in Table 3.1.

| Model[a] | AIC[a] | ΔAIC[b] | $w_i$[c] | $K$[d] |
|---|---|---|---|---|
| ψ (HTSP+AREA+LAND) | 171.43 | 0.00 | 0.21 | 5 |
| ψ (HTSP+AREA) | 171.78 | 0.35 | 0.18 | 4 |
| ψ (AREA) | 172.25 | 0.82 | 0.14 | 3 |
| ψ (AREA+LAND) | 172.30 | 0.88 | 0.14 | 4 |
| ψ (HTSP+AREA+EVOW+LAND) | 173.08 | 1.65 | 0.09 | 6 |
| ψ (HTSP+AREA+EVOW) | 173.54 | 2.11 | 0.07 | 5 |
| ψ (AREA+EVOW+LAND) | 173.62 | 2.20 | 0.07 | 5 |
| ψ (AREA+EVOW) | 173.77 | 2.34 | 0.07 | 4 |
| ψ (HTSP+LAND) | 176.79 | 5.36 | 0.01 | 4 |
| ψ (HTSP) | 178.28 | 6.86 | 0.01 | 3 |
| ψ (HTSP+EVOW+LAND) | 178.55 | 7.12 | 0.01 | 5 |
| ψ (LAND) | 179.13 | 7.70 | 0.00 | 3 |
| ψ (.) | 179.62 | 8.19 | 0.00 | 2 |
| ψ (HTSP+EVOW) | 180.16 | 8.73 | 0.00 | 4 |
| ψ (EVOW+LAND) | 180.48 | 9.05 | 0.00 | 4 |
| ψ (EVOW) | 181.20 | 9.78 | 0.00 | 3 |

[a] Models are denoted as additive (+); Variables are defined in Table 3.1.

[b] Akaike's Information Criterion.

[c] Difference in AICc relative to smallest value.

[d] Akaike's weight of models.

[e] Number of parameters.

Table 3.8 - Summary of the candidate model set ranked by AIC with the best-approximating model at the top for breeding pied-billed grebe occupancy probability (ψ) with constant detection probability *p*(.), Saskatchewan, 2011. Variable names used in models are defined in Table 3.1.

| Model[a] | AIC[a] | ΔAIC[b] | $w_i$[c] | $K$[d] |
|---|---|---|---|---|
| ψ (AREA+EVOW+EVOW2+LAND) | 153.65 | 0.00 | 0.32 | 6 |
| ψ (HTSP+AREA+EVOW+EVOW2+LAND) | 154.16 | 0.52 | 0.24 | 7 |
| ψ (HTSP+AREA+EVOW+EVOW2) | 154.82 | 1.17 | 0.18 | 6 |
| ψ (AREA+EVOW+EVOW2) | 155.75 | 2.10 | 0.11 | 5 |
| ψ (HTSP+AREA) | 156.93 | 3.29 | 0.06 | 4 |
| ψ (HTSP+AREA+LAND) | 157.80 | 4.15 | 0.04 | 5 |
| ψ (AREA) | 158.46 | 4.82 | 0.03 | 3 |
| ψ (AREA+LAND) | 158.66 | 5.01 | 0.03 | 4 |
| ψ (HTSP+EVOW+EVOW2) | 166.87 | 13.23 | 0.00 | 5 |
| ψ (EVOW+EVOW2) | 167.73 | 14.08 | 0.00 | 4 |
| ψ (HTSP+EVOW+EVOW2+LAND) | 168.77 | 15.12 | 0.00 | 6 |
| ψ (EVOW+EVOW2+LAND) | 169.19 | 15.55 | 0.00 | 5 |
| ψ (HTSP) | 171.72 | 18.08 | 0.00 | 3 |
| ψ (.) | 172.87 | 19.23 | 0.00 | 2 |
| ψ (HTSP+LAND) | 173.71 | 20.07 | 0.00 | 4 |
| ψ (LAND) | 174.76 | 21.12 | 0.00 | 3 |

[a] Models are denoted as additive (+); Variables are defined in Table 3.1.

[b] Akaike's Information Criterion.

[c] Difference in AICc relative to smallest value.

[d] Akaike's weight of models.

[e] Number of parameters.

Table 3.9 - Summary of the candidate model set ranked by AIC with the best-approximating model at the top for pied-billed grebe brood occupancy probability (ψ) with constant detection probability *p*(.), Saskatchewan, 2010. Variable names used in models are defined in Table 3.1.

| Model[a] | AIC[a] | ΔAIC[b] | $w_i$[c] | $K$[d] |
|---|---|---|---|---|
| ψ (HTSP+AREA+LAND) | 210.63 | 0.00 | 0.28 | 5 |
| ψ (HTSP+LAND) | 211.30 | 0.67 | 0.20 | 4 |
| ψ (HTSP+AREA+EVOW+EVOW2+LAND) | 211.64 | 1.01 | 0.17 | 7 |
| ψ (HTSP+EVOW+EVOW2+LAND) | 211.93 | 1.29 | 0.15 | 6 |
| ψ (AREA+LAND) | 214.02 | 3.39 | 0.05 | 4 |
| ψ (AREA+EVOW+EVOW2+LAND) | 214.30 | 3.67 | 0.05 | 6 |
| ψ (EVOW+EVOW2+LAND) | 215.75 | 5.11 | 0.02 | 5 |
| ψ (HTSP+AREA+EVOW+EVOW2) | 216.00 | 5.37 | 0.02 | 6 |
| ψ (LAND) | 216.55 | 5.92 | 0.01 | 3 |
| ψ (HTSP+EVOW+EVOW2) | 216.80 | 6.17 | 0.01 | 5 |
| ψ (HTSP+AREA) | 216.88 | 6.25 | 0.01 | 4 |
| ψ (AREA+EVOW+EVOW2) | 218.29 | 7.66 | 0.01 | 5 |
| ψ (AREA) | 219.58 | 8.95 | 0.00 | 3 |
| ψ (HTSP) | 219.64 | 9.00 | 0.00 | 3 |
| ψ (EVOW+EVOW2) | 219.97 | 9.33 | 0.00 | 4 |
| ψ (.) | 223.70 | 13.07 | 0.00 | 2 |

[a] Models are denoted as additive (+); Variables are defined in Table 3.1.

[b] Akaike's Information Criterion.

[c] Difference in AICc relative to smallest value.

[d] Akaike's weight of models.

[e] Number of parameters.

Table 3.10 - Summary of the candidate model set ranked by AIC with the best-approximating model at the top for pied-billed grebe brood occupancy probability (ψ) with constant detection probability *p*(.), Saskatchewan, 2011. Variable names used in models are defined in Table 3.1.

| Model[a] | AIC[a] | ΔAIC[b] | $w_i$[c] | $K$[d] |
|---|---|---|---|---|
| ψ (AREA*EVOW+EVOW2+LAND) | 194.68 | 0.00 | 0.64 | 7 |
| ψ (HTSP+AREA+EVOW+EVOW2+LAND) | 197.23 | 2.55 | 0.18 | 7 |
| ψ (HTSP+AREA*EVOW+EVOW2) | 199.77 | 5.09 | 0.05 | 7 |
| ψ (AREA*EVOW+EVOW2) | 199.79 | 5.11 | 0.05 | 6 |
| ψ (AREA+LAND) | 200.46 | 5.78 | 0.04 | 4 |
| ψ (HTSP+AREA+LAND) | 200.93 | 6.25 | 0.03 | 5 |
| ψ (AREA) | 206.07 | 11.39 | 0.00 | 3 |
| ψ (HTSP+AREA) | 206.17 | 11.49 | 0.00 | 4 |
| ψ (EVOW+EVOW2+LAND) | 206.18 | 11.49 | 0.00 | 5 |
| ψ (HTSP+EVOW+EVOW2+LAND) | 207.01 | 12.33 | 0.00 | 6 |
| ψ (EVOW+EVOW2) | 207.44 | 12.76 | 0.00 | 4 |
| ψ (HTSP+EVOW+EVOW2) | 207.57 | 12.89 | 0.00 | 5 |
| ψ (LAND) | 211.92 | 17.24 | 0.00 | 3 |
| ψ (HTSP+LAND) | 212.76 | 18.08 | 0.00 | 4 |
| ψ (.) | 213.69 | 19.01 | 0.00 | 2 |
| ψ (HTSP) | 214.01 | 19.33 | 0.00 | 3 |

[a] Models are denoted as additive (+) and/or multiplicative (*); Variables are defined in Table 3.1.

[b] Akaike's Information Criterion.

[c] Difference in AICc relative to smallest value.

[d] Akaike's weight of models.

[e] Number of parameters.

Table 3.11 - Summary of cumulative model weights ($\sum AICw_i$) for breeding adult horned and pied-billed grebes and broods in the Canadian PPR in 2010 and 2011(sum of AIC weight for each model that contains a specific variable).

| | HOGR | | PBGR | |
|---|---|---|---|---|
| Variable[a] | 2010 | 2011 | 2010 | 2011 |
| *Adults*: | | | | |
| EVOW | 0.609 | 1.000 | 0.292 | 0.814 |
| AREA | 0.299 | 0.376 | 0.956 | 0.999 |
| HTSP | 0.643 | 0.873 | 0.557 | 0.500 |
| LAND | 0.580 | 0.841 | 0.509 | 0.595 |
| *Broods*: | | | | |
| EVOW | 0.256 | 0.879 | 0.378 | 0.910 |
| AREA | 0.431 | 0.259 | 0.572 | 0.993 |
| HTSP | 0.909 | 0.414 | 0.845 | 0.264 |
| LAND | 0.716 | 0.631 | 0.937 | 0.887 |

[a] Variables are defined in Table 3.1.

## Figures 3.6

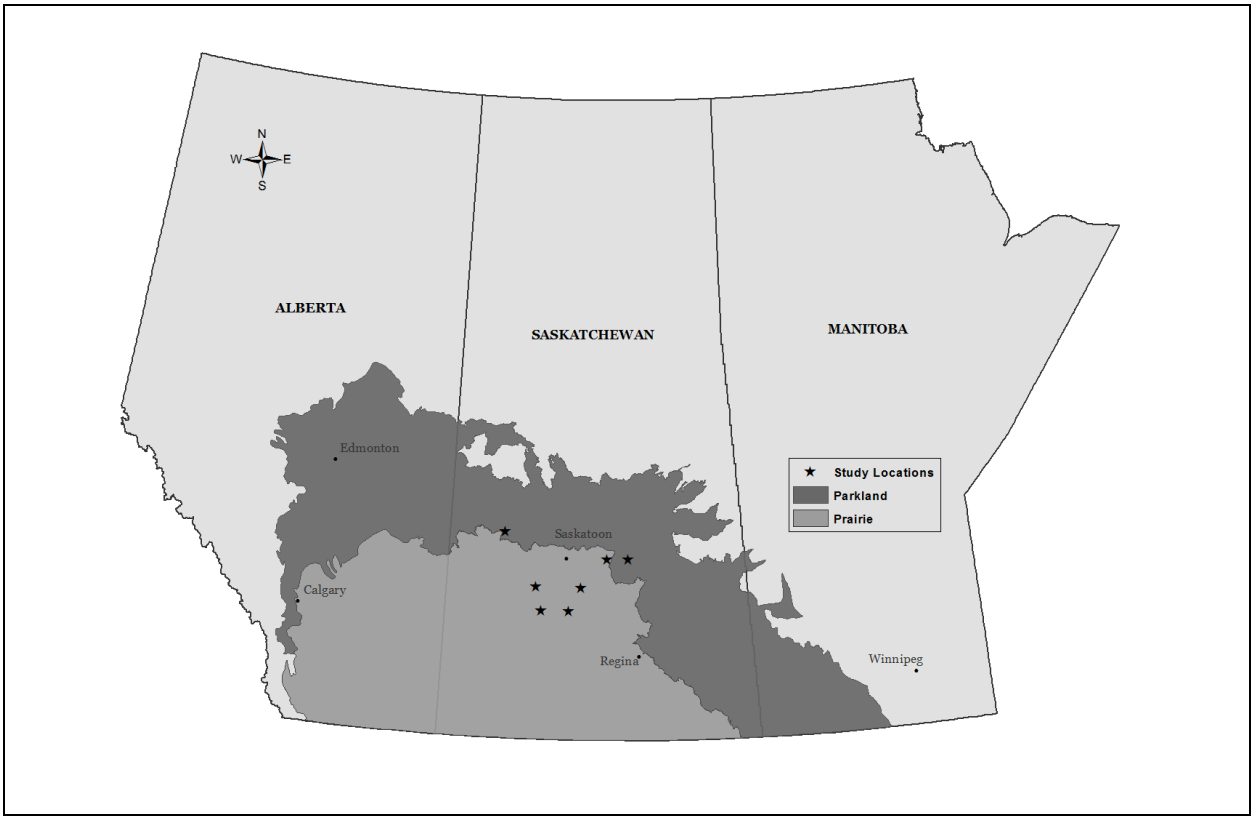


**Figure 3.1** - Study sites within Saskatchewan, Canadian Prairie Pothole Region. Also shown are the prairie and parkland ecoregions.

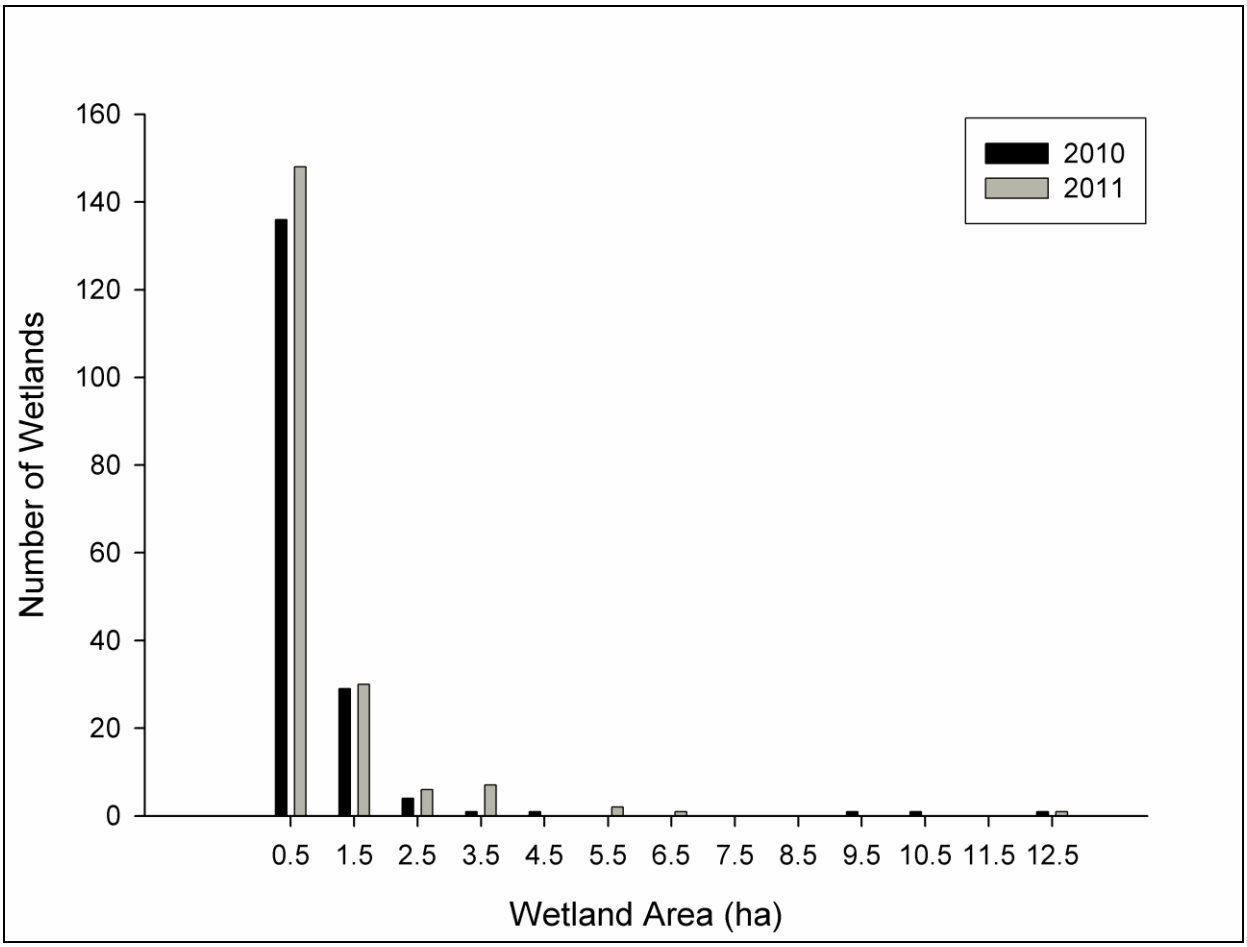


**Figure 3.2** - Distribution of wetlands by area (ha) on all study sites in Saskatchewan, 2010 and 2011. The category 0.5 ha includes wetlands ranging in area from 0.1 to 0.99 ha.

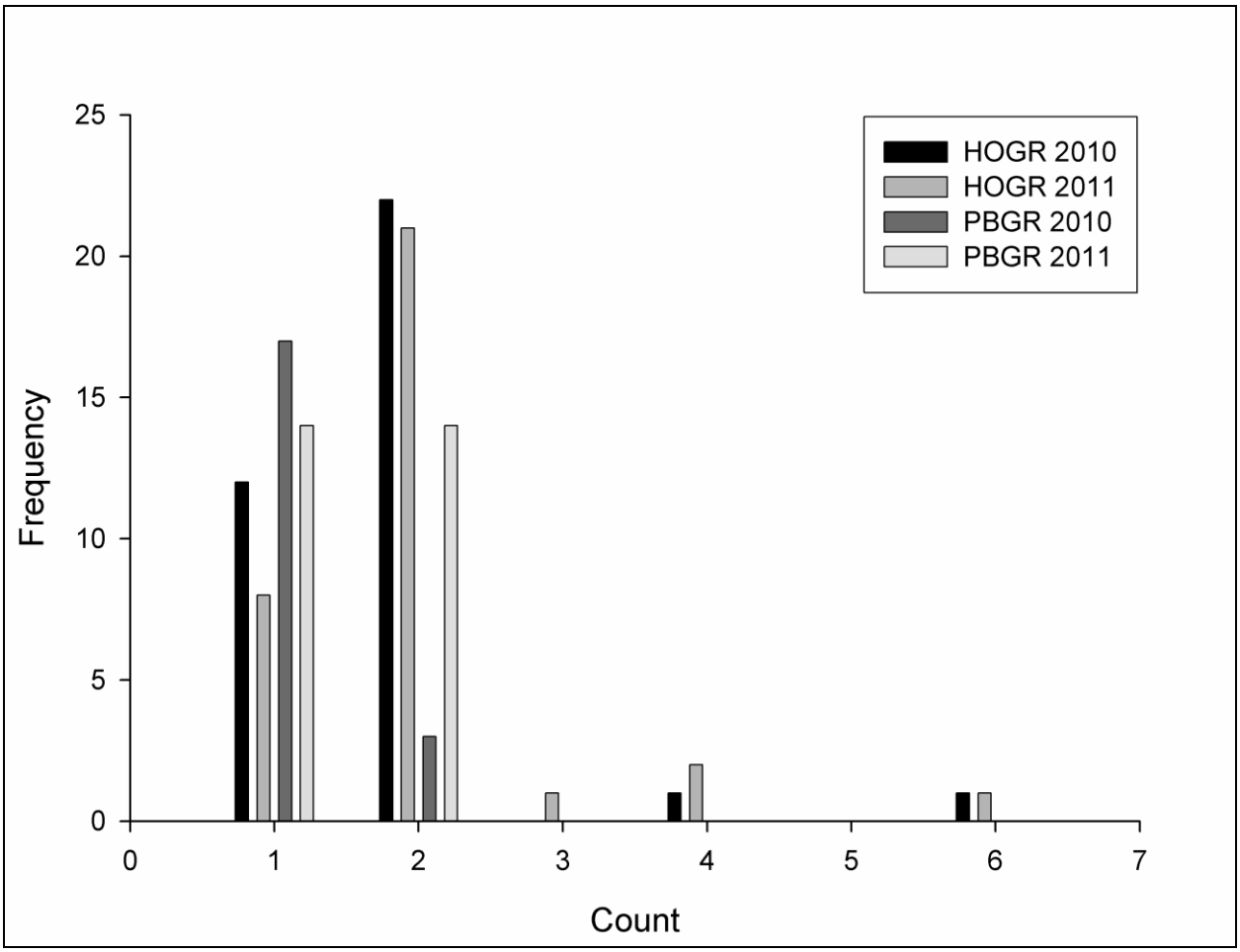


**Figure 3.3** Frequency distributions of counts of breeding adult horned (HOGR) and pied-billed (PBGR) grebes recorded on wetlands in southcentral Saskatchewan, 2010 and 2011.

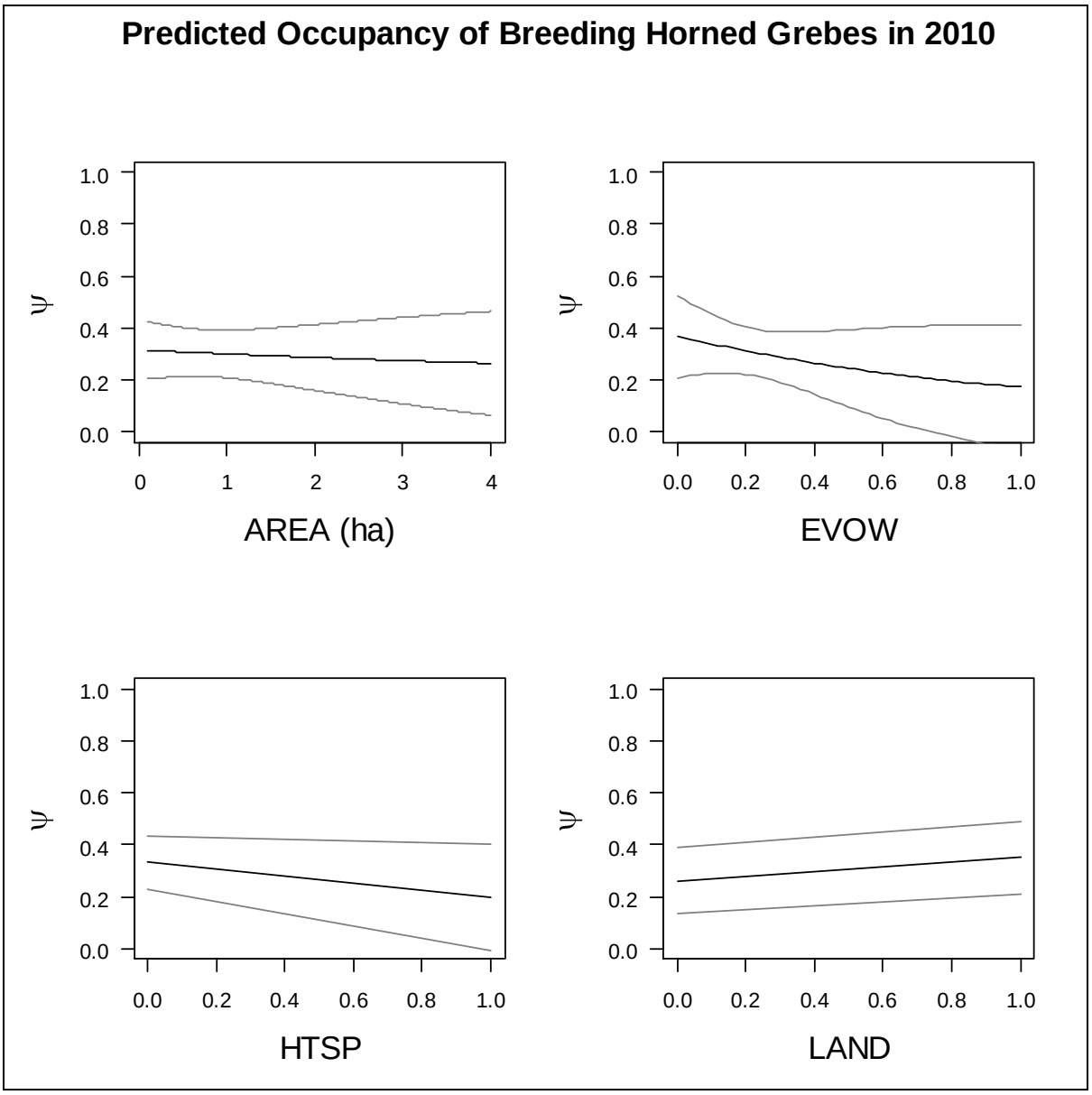


**Figure 3.4** Model-averaged predictions of occupancy probability (ψ) and 95% confidence intervals (gray lines) in relation to key variables for breeding horned grebes in 2010. Variables are AREA (wetland area in hectares), EVOW (ratio of the proportion of emergent vegetation to open water), HTSP (binary; presence (1) or absence (0) of heterospecific species), and LAND (binary; landscapes with relatively low (0) and high (1) wetland densities). Cumulative AIC model weights for each variable are shown in Table 3.11.

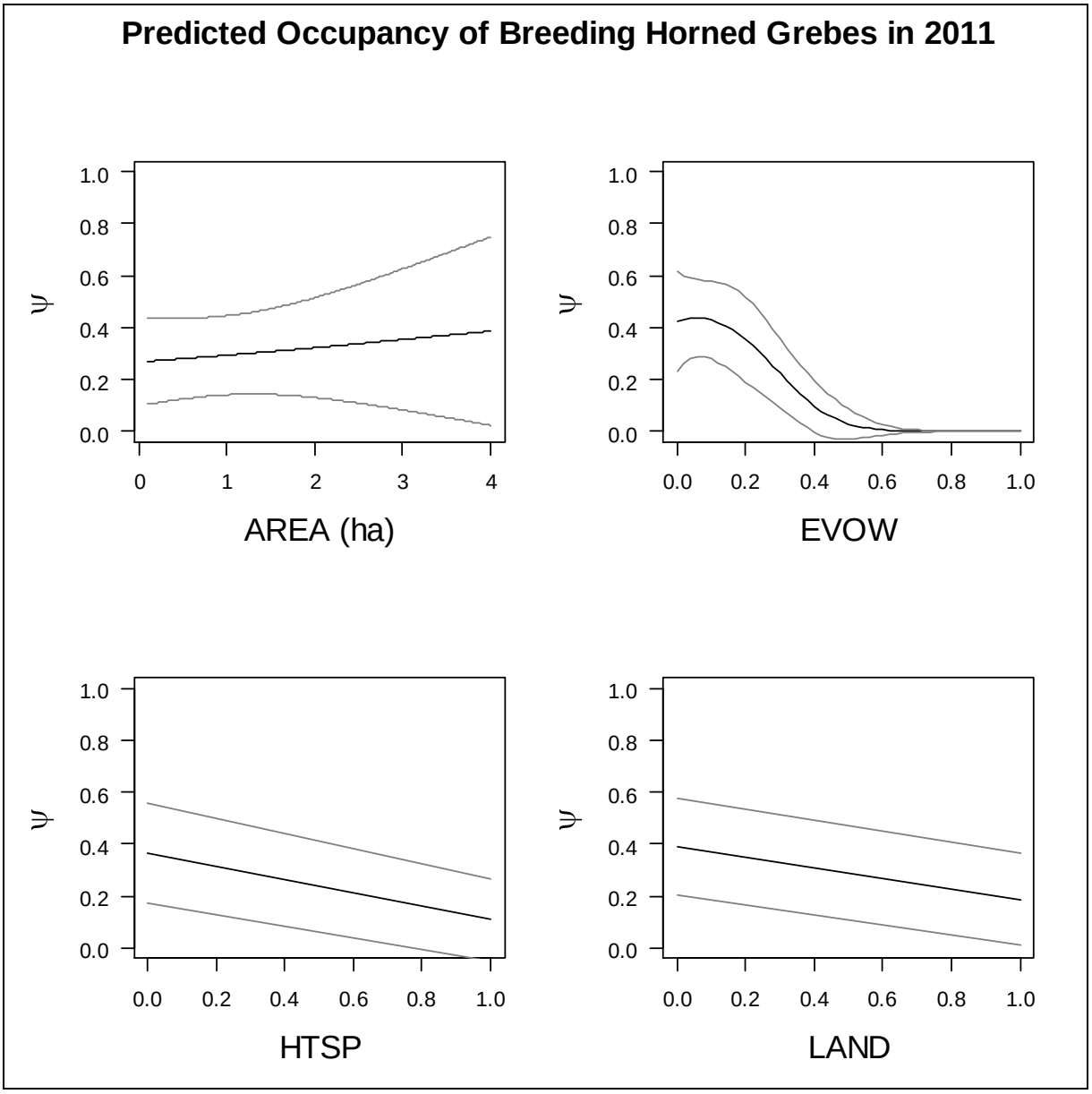


**Figure 3.5** Model-averaged predictions of occupancy probability (ψ) and 95% confidence intervals (gray lines) in relation to key variables for breeding horned grebes in 2011. Variables are AREA (wetland area in hectares), EVOW (ratio of the proportion of emergent vegetation to open water), HTSP (binary; presence (1) or absence (0) of heterospecific species), and LAND (binary; landscapes with relatively low (0) and high (1) wetland densities). Cumulative AIC model weights for each variable are shown in Table 3.11.

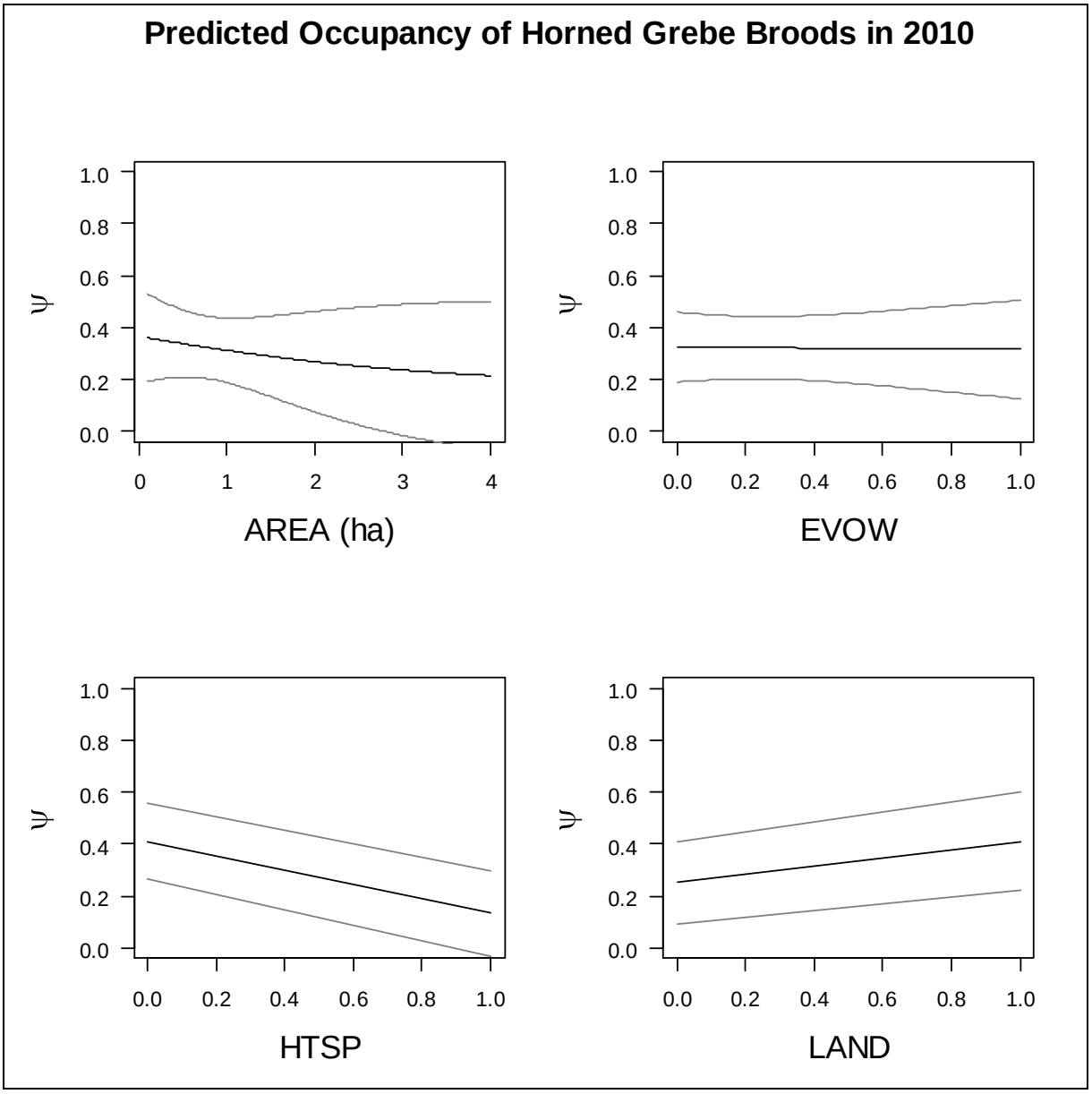


**Figure 3.6** Model-averaged predictions of occupancy probability (ψ) and 95% confidence intervals (gray lines) in relation to key variables for horned grebe broods in 2010. Variables are AREA (wetland area in hectares), EVOW (ratio of the proportion of emergent vegetation to open water), HTSP (binary; presence (1) or absence (0) of heterospecific species), and LAND (binary; landscapes with relatively low (0) and high (1) wetland densities). Cumulative AIC model weights for each variable are shown in Table 3.11.

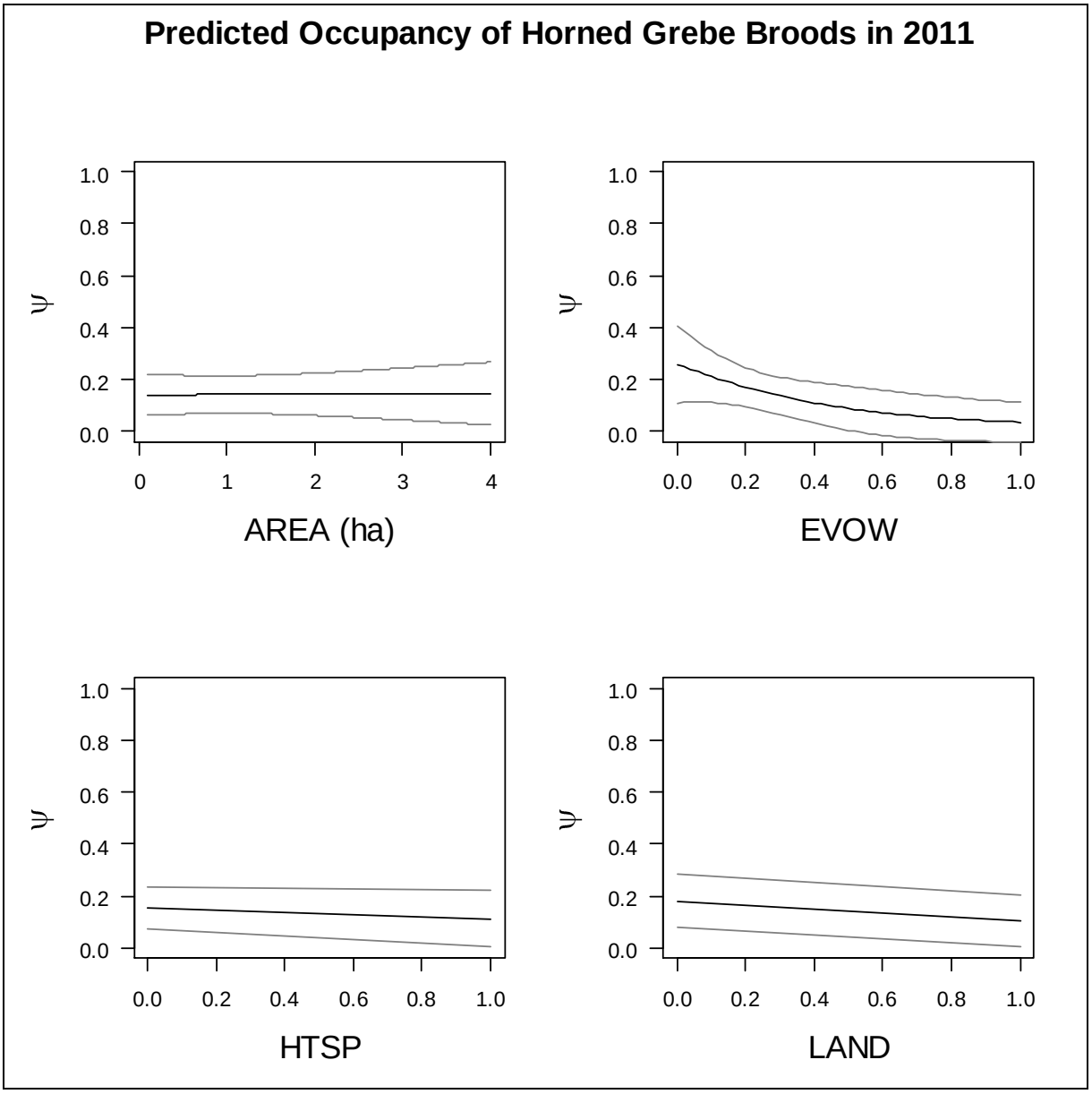


**Figure 3.7** Model-averaged predictions of occupancy probability (ψ) and 95% confidence intervals (gray lines) in relation to key variables for horned grebe broods in 2011. Variables are AREA (wetland area in hectares), EVOW (ratio of the proportion of emergent vegetation to open water), HTSP (binary; presence (1) or absence (0) of heterospecific species), and LAND (binary; landscapes with relatively low (0) and high (1) wetland densities). Cumulative AIC model weights for each variable are shown in Table 3.11.

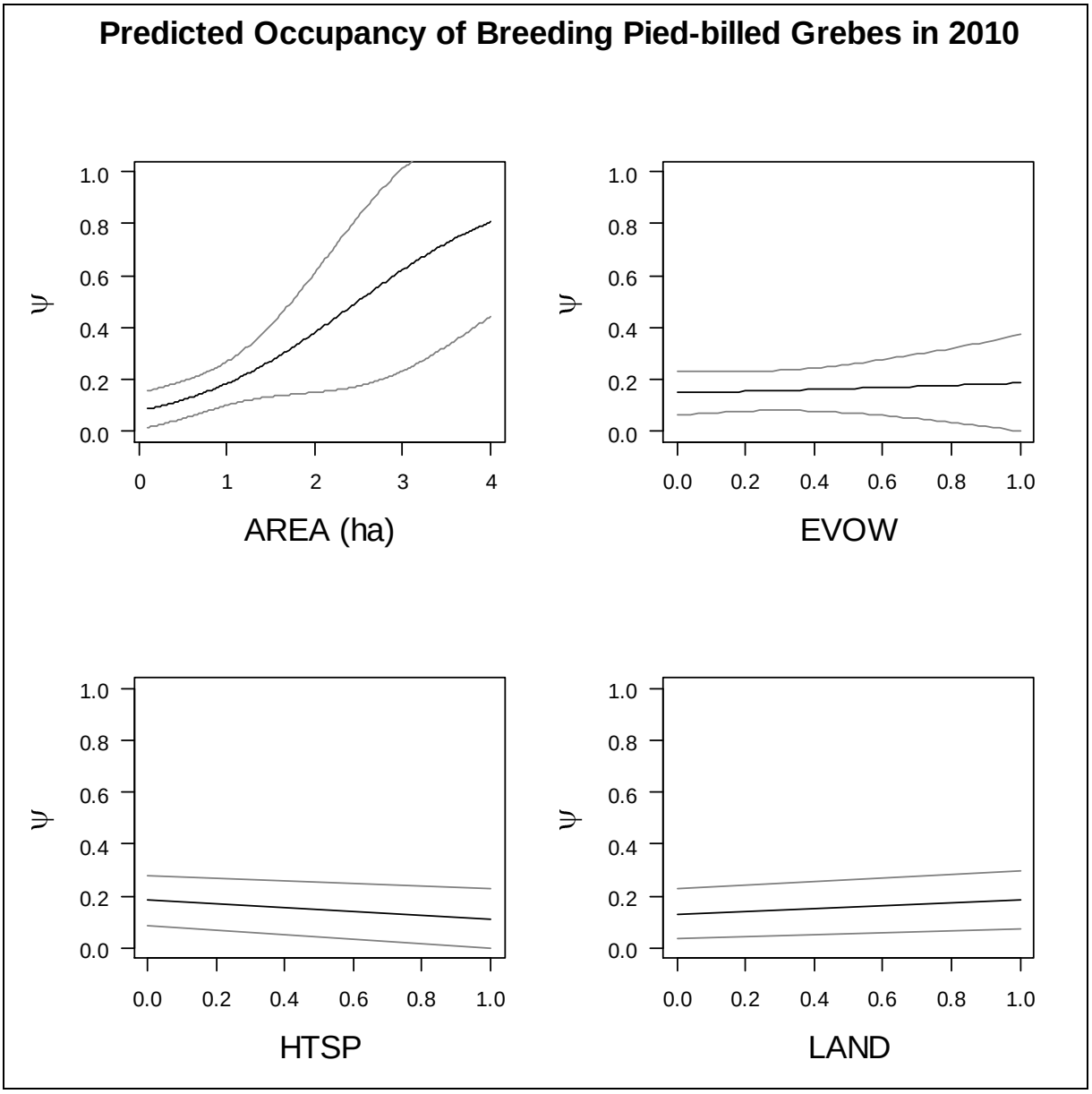


**Figure 3.8** Model-averaged predictions of occupancy probability (ψ) and 95% confidence intervals (gray lines) in relation to key variables for breeding pied-billed grebes in 2010. Variables are AREA (wetland area in hectares), EVOW (ratio of the proportion of emergent vegetation to open water), HTSP (binary; presence (1) or absence (0) of heterospecific species), and LAND (binary; landscapes with relatively low (0) and high (1) wetland densities). Cumulative AIC model weights for each variable are shown in Table 3.11.

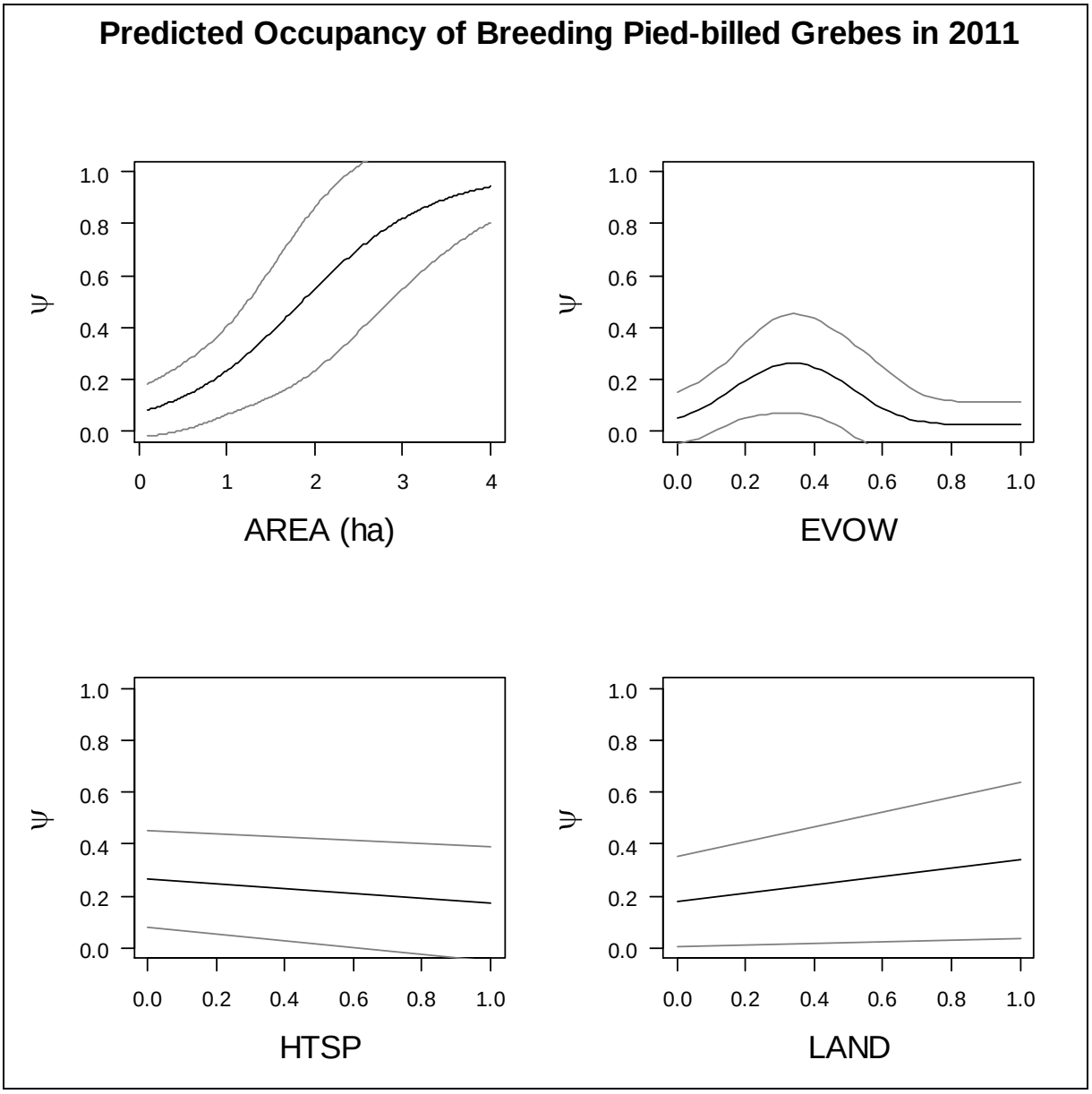


**Figure 3.9** Model-averaged predictions of occupancy probability (ψ) and 95% confidence intervals (gray lines) in relation to key variables for breeding pied-billed grebes in 2011. Variables are AREA (wetland area in hectares), EVOW (ratio of the proportion of emergent vegetation to open water), HTSP (binary; presence (1) or absence (0) of heterospecific species), and LAND (binary; landscapes with relatively low (0) and high (1) wetland densities). Cumulative AIC model weights for each variable are shown in Table 3.11.

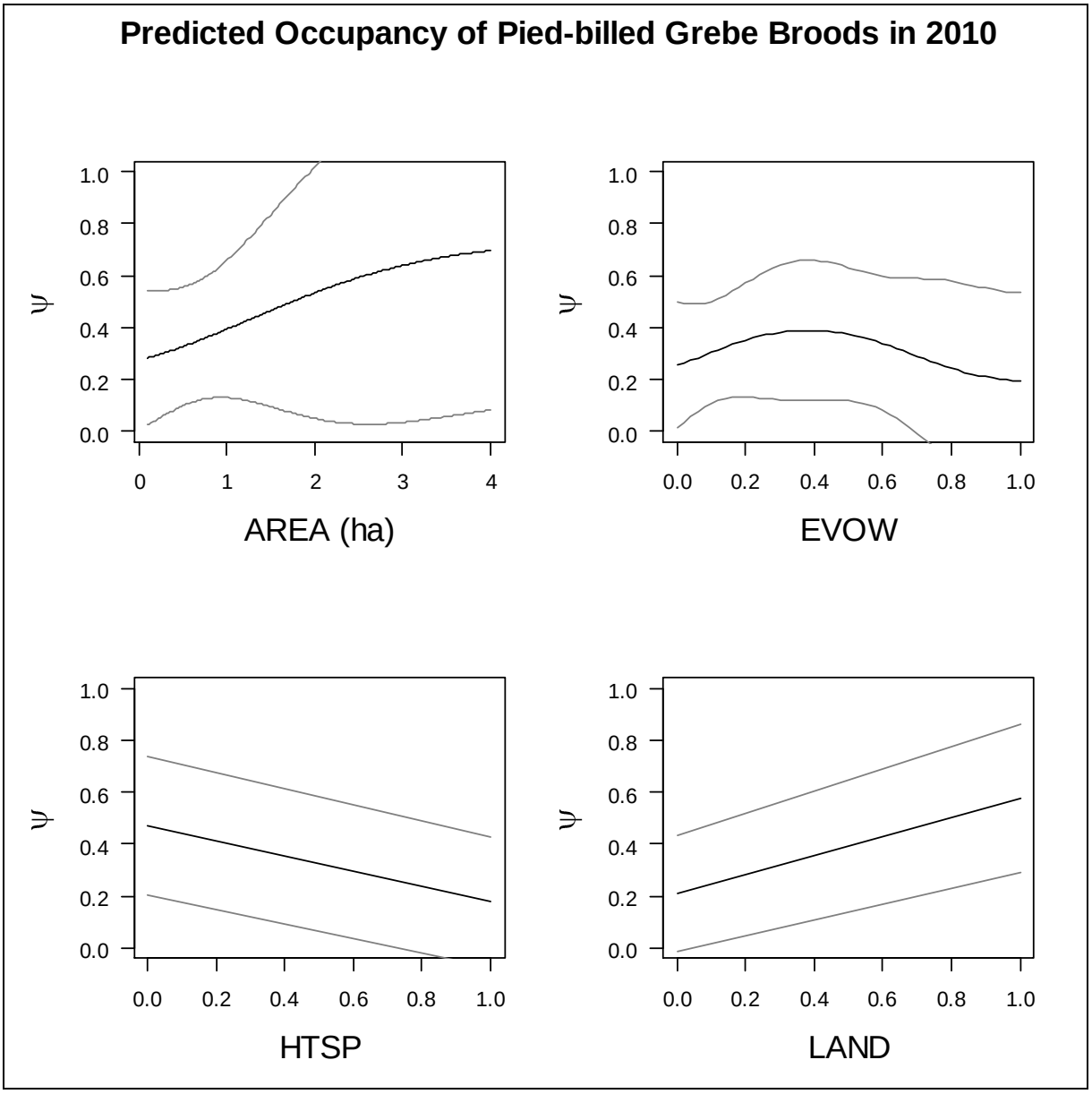


**Figure 3.10** Model-averaged predictions of occupancy probability (ψ) and 95% confidence intervals (gray lines) in relation to key variables for pied-billed grebe broods in 2010. Variables are AREA (wetland area in hectares), EVOW (ratio of the proportion of emergent vegetation to open water), HTSP (binary; presence (1) or absence (0) of heterospecific species), and LAND (binary; landscapes with relatively low (0) and high (1) wetland densities). Cumulative AIC model weights for each variable are shown in Table 3.11.

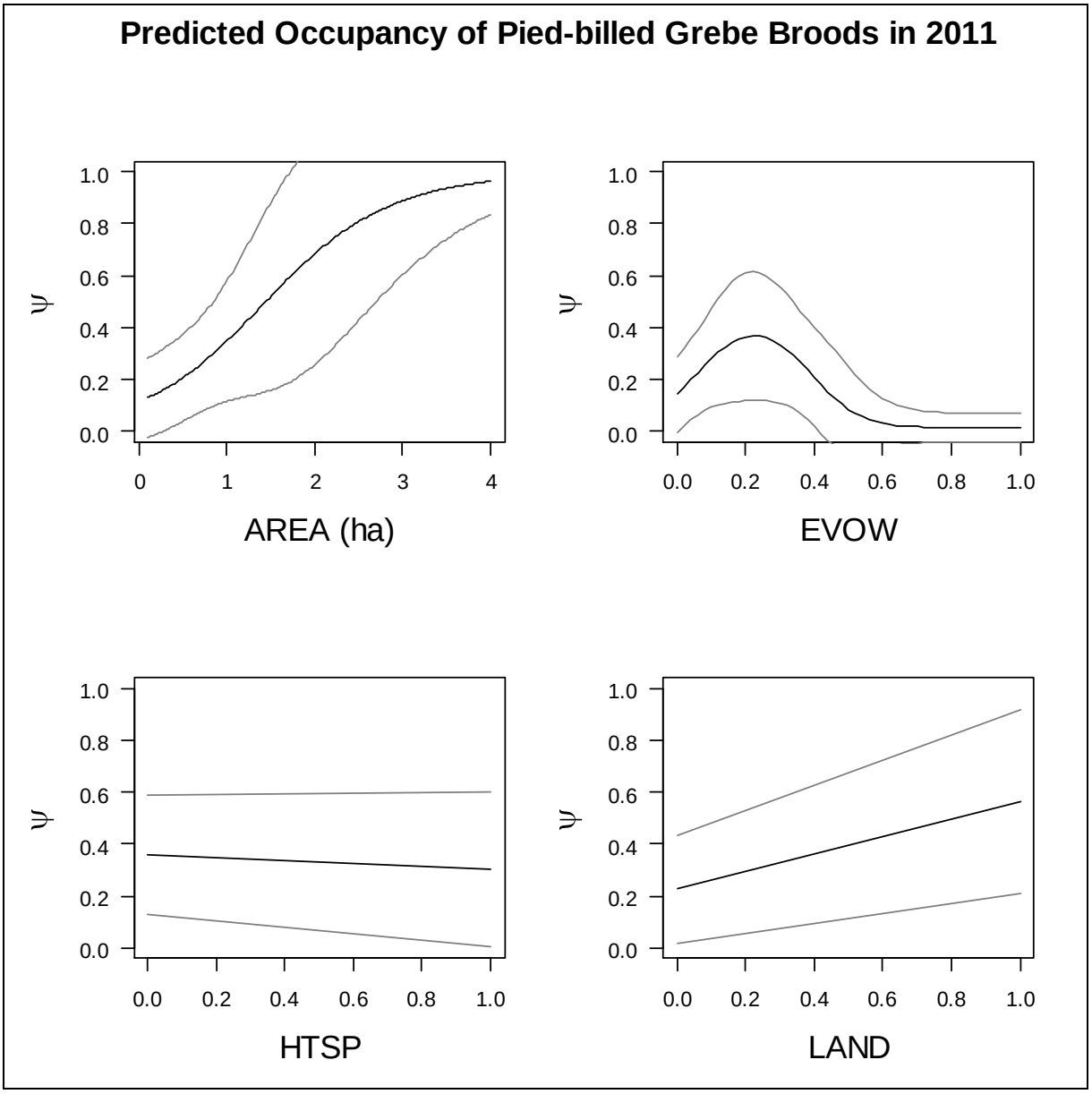


**Figure 3.11** Model-averaged predictions of occupancy probability (ψ) and 95% confidence intervals (gray lines) in relation to key variables for pied-billed grebe broods in 2011. Variables are AREA (wetland area in hectares), EVOW (ratio of the proportion of emergent vegetation to open water), HTSP (binary; presence (1) or absence (0) of heterospecific species), and LAND (binary; landscapes with relatively low (0) and high (1) wetland densities). Cumulative AIC model weights for each variable are shown in Table 3.11.

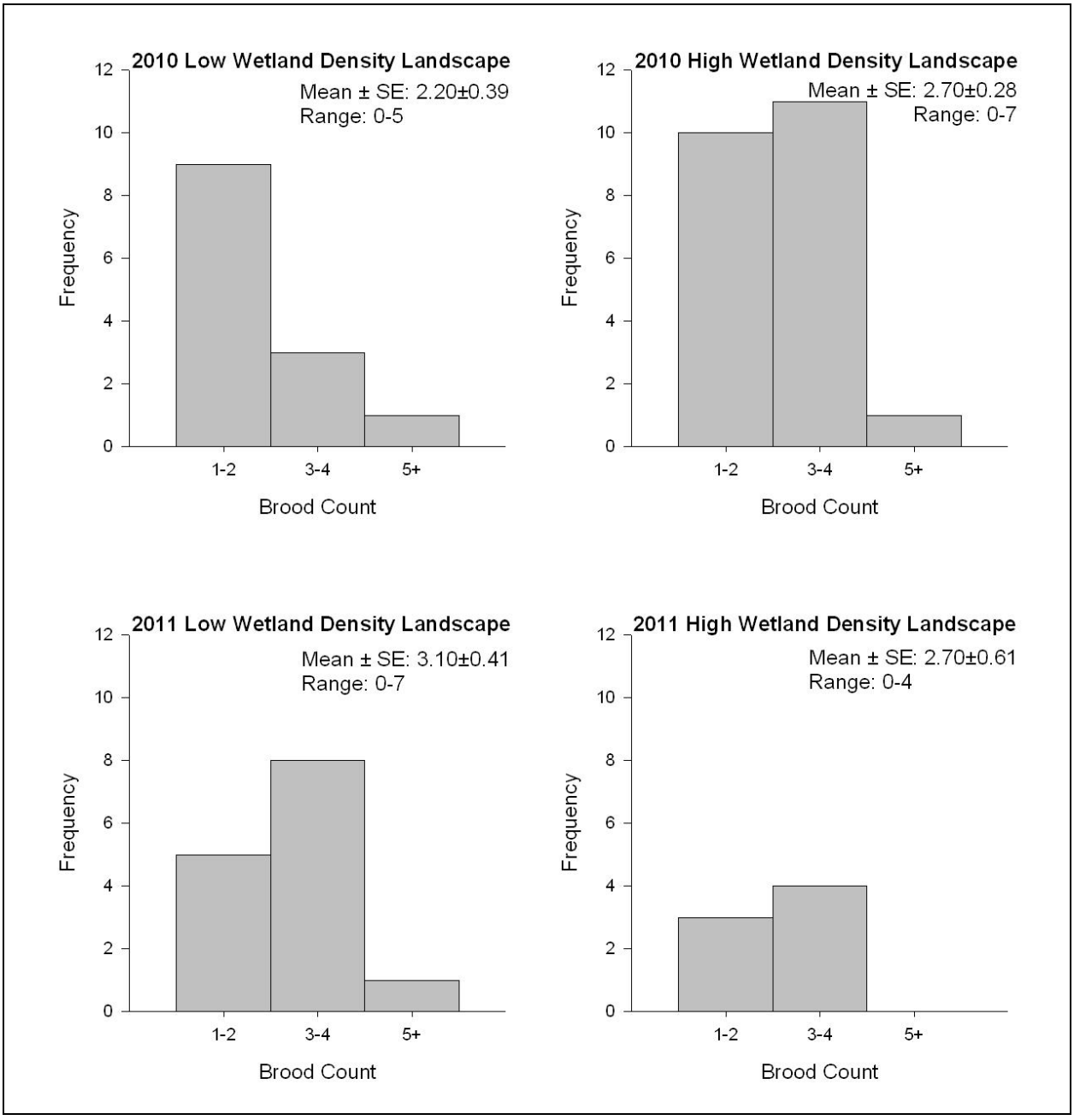


**Figure 3.12** Distribution of horned grebe brood counts (maximum count over 3 visits; not adjusted for detection probability) in low and high wetland density landscapes in Saskatchewan, 2010 (n = 112 wetlands) and 2011 (n=115 wetlands).

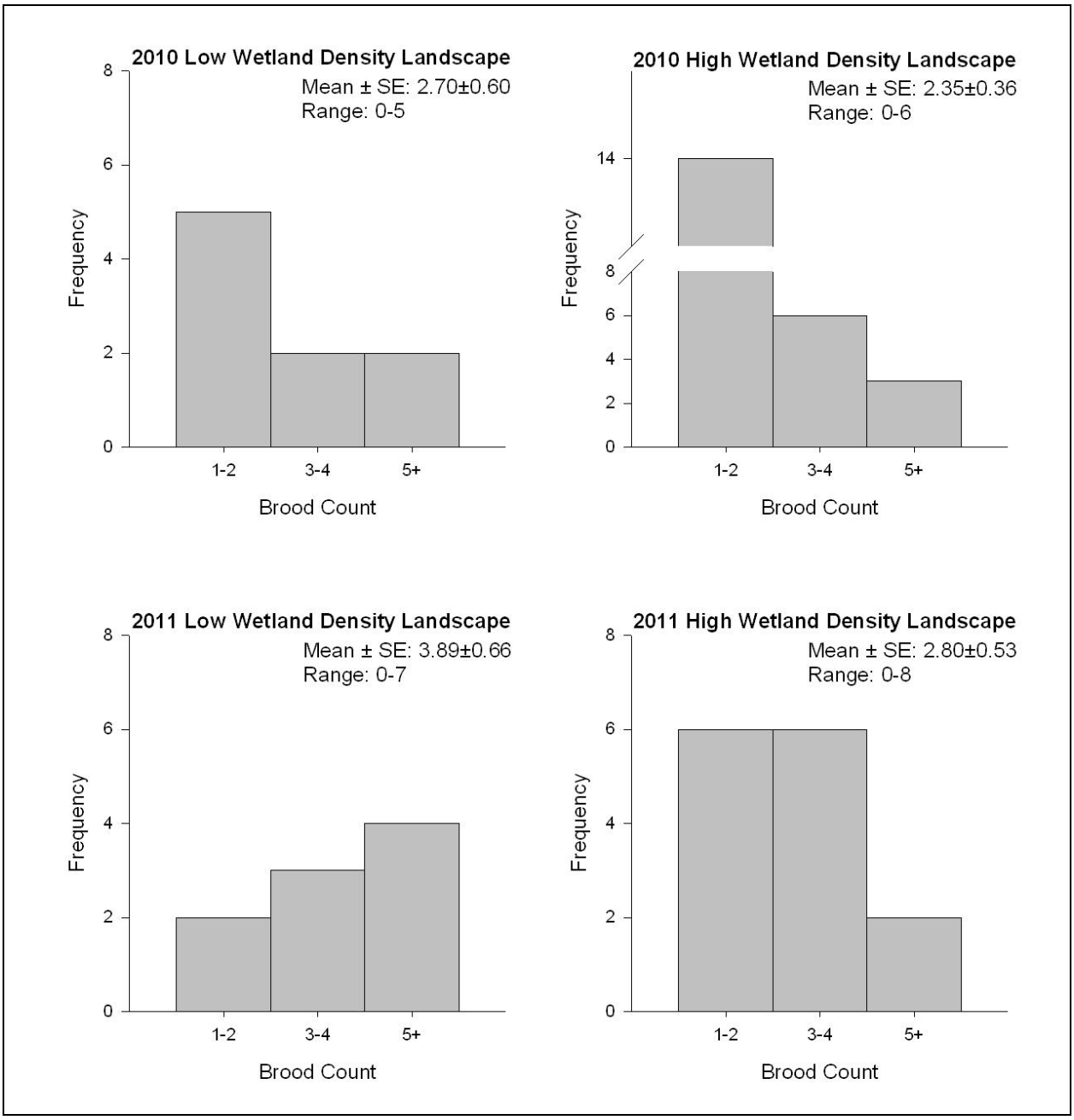


**Figure 3.13** Distribution of pied-billed grebe brood counts (maximum count over 3 visits; not adjusted for detection probability) in low and high wetland density landscapes in Saskatchewan, 2010 (n = 112 wetlands) and 2011 (n=115 wetlands).

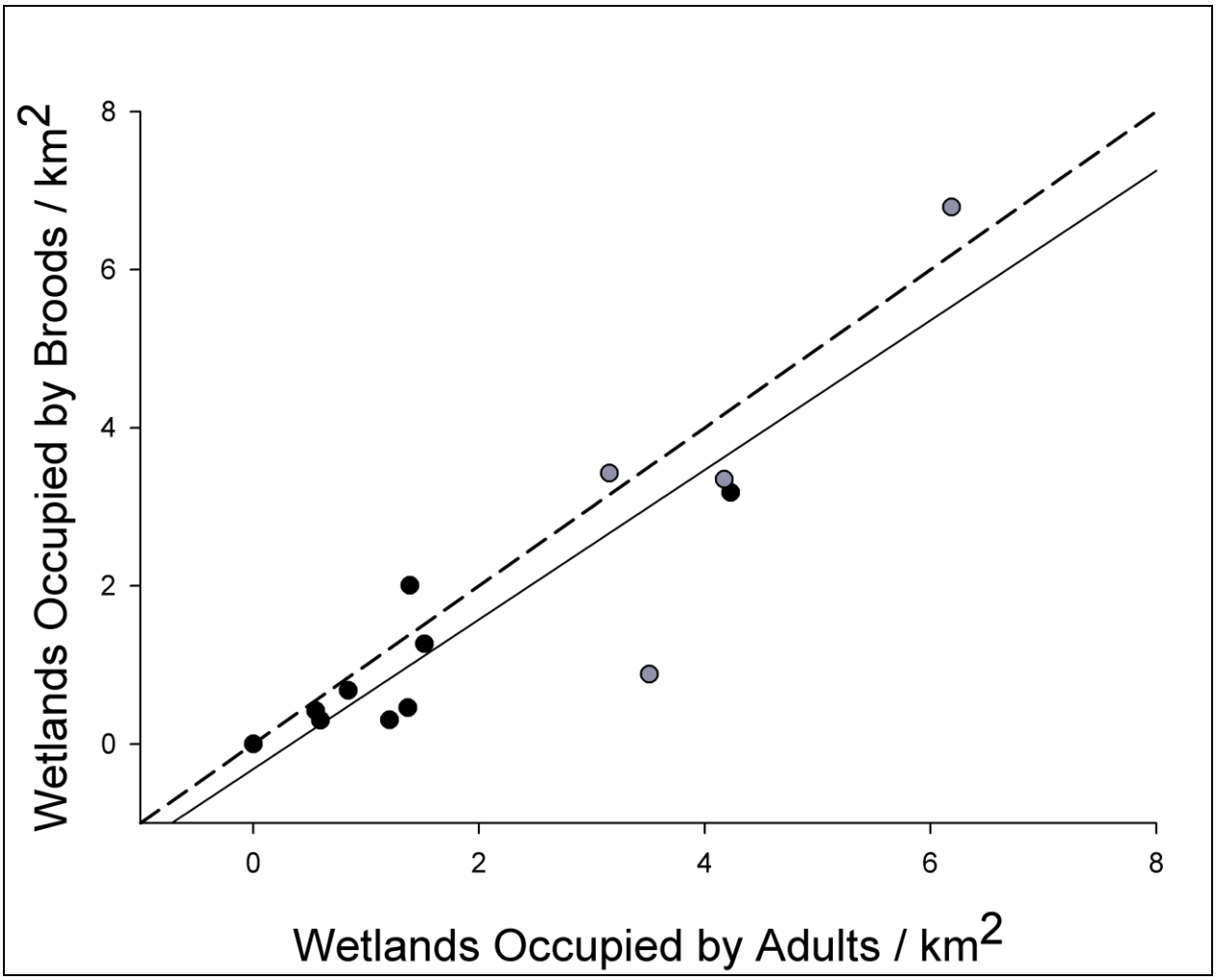


**Figure 3.14** The relationship between observed densities of breeding horned grebe adults and broods for study sites in 2010 and 2011. The solid line describes the observed relationship as determined by least-squares regression ($r^2$=0.81) and the dashed line describes a predicted null relationship of the slope = 1.0. Density is calculated as the occupancy probability of a breeding adult or brood weighted by the total number of wetlands at each site. Grey points indicate high wetland density landscape study sites.

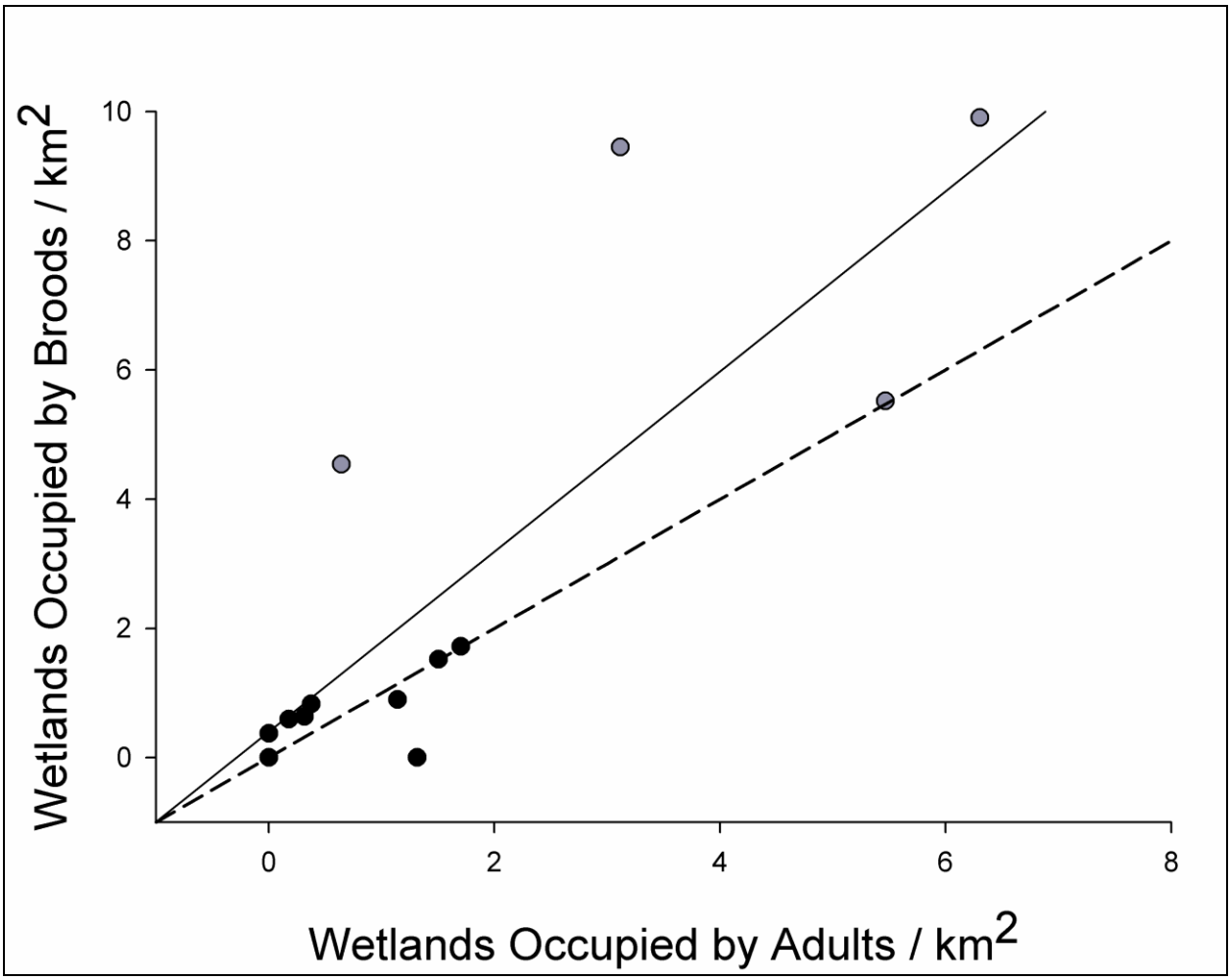


**Figure 3.15** The relationship between observed densities of breeding pied-billed grebe adults and broods for study sites in 2010 and 2011. The solid line describes the observed relationship as determined by least-squares regression ($r^2$=0.67) and the dashed line describes a predicted null relationship of the slope = 1.0. Density is calculated as the occupancy probability of a breeding adult or brood weighted by the total number of wetlands at each site. Grey points indicate high wetland density landscape study sites.

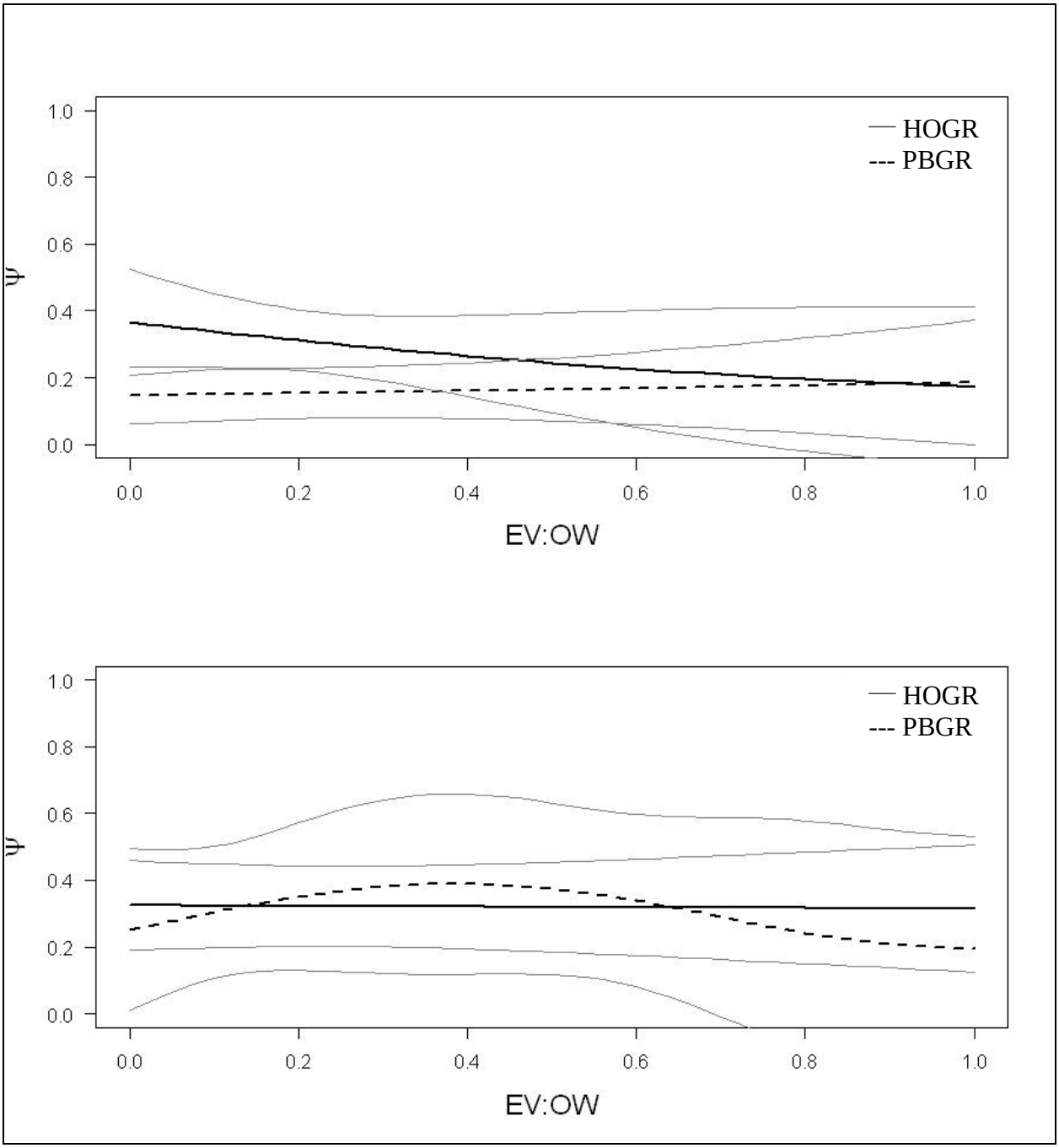


**Figure 3.16** Model-averaged occupancy probability prediction for breeding horned and pied-billed grebe adults (top) and broods (bottom) in relation to the ratio of emergent vegetation to open water (EVOW; Table 3.1) in 2010.

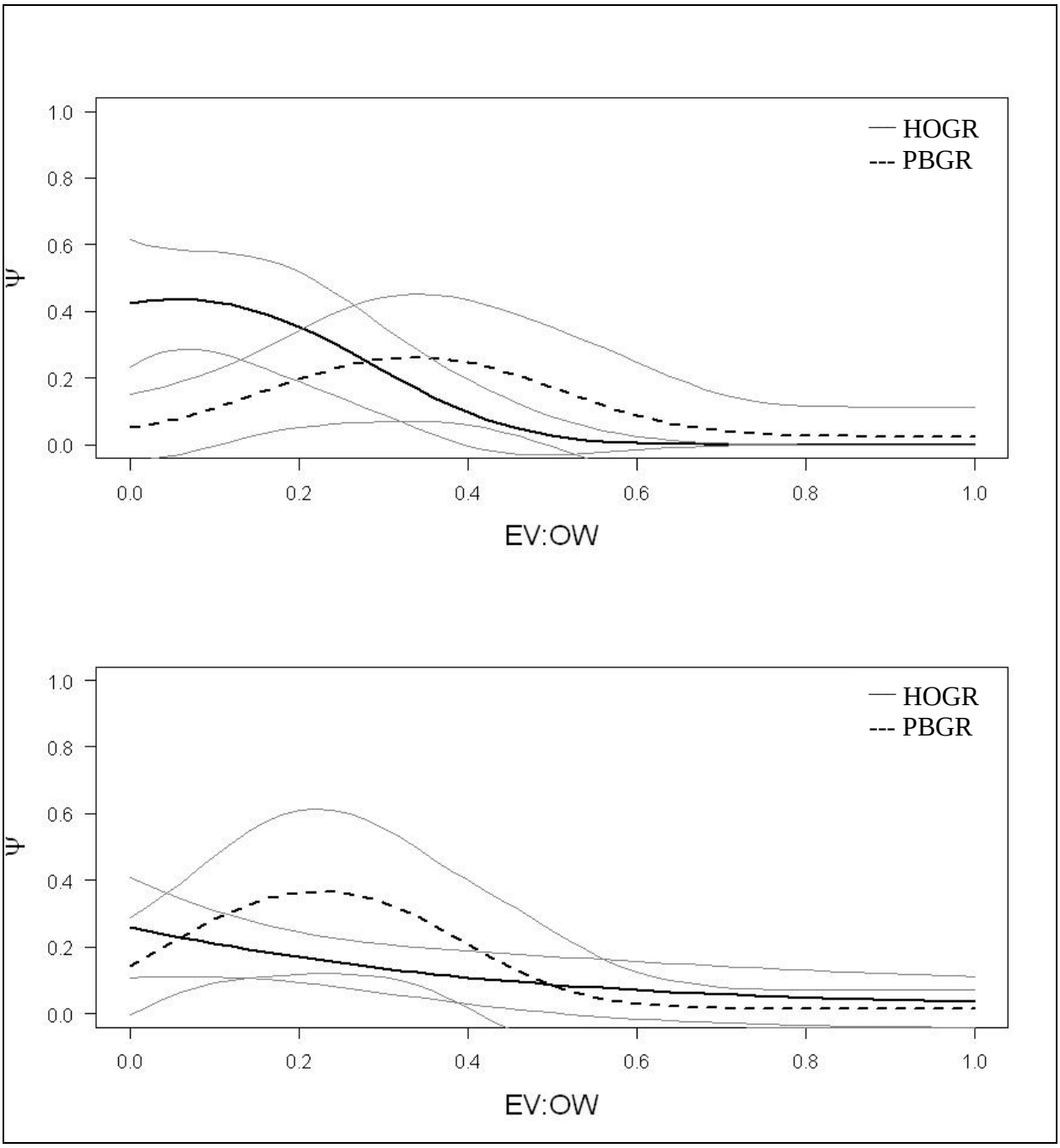


**Figure 3.17** Model-averaged occupancy probability prediction for breeding horned and pied-billed grebe adults (top) and broods (bottom) in relation to the ratio of emergent vegetation to open water (EVOW; Table 3.1) in 2011.

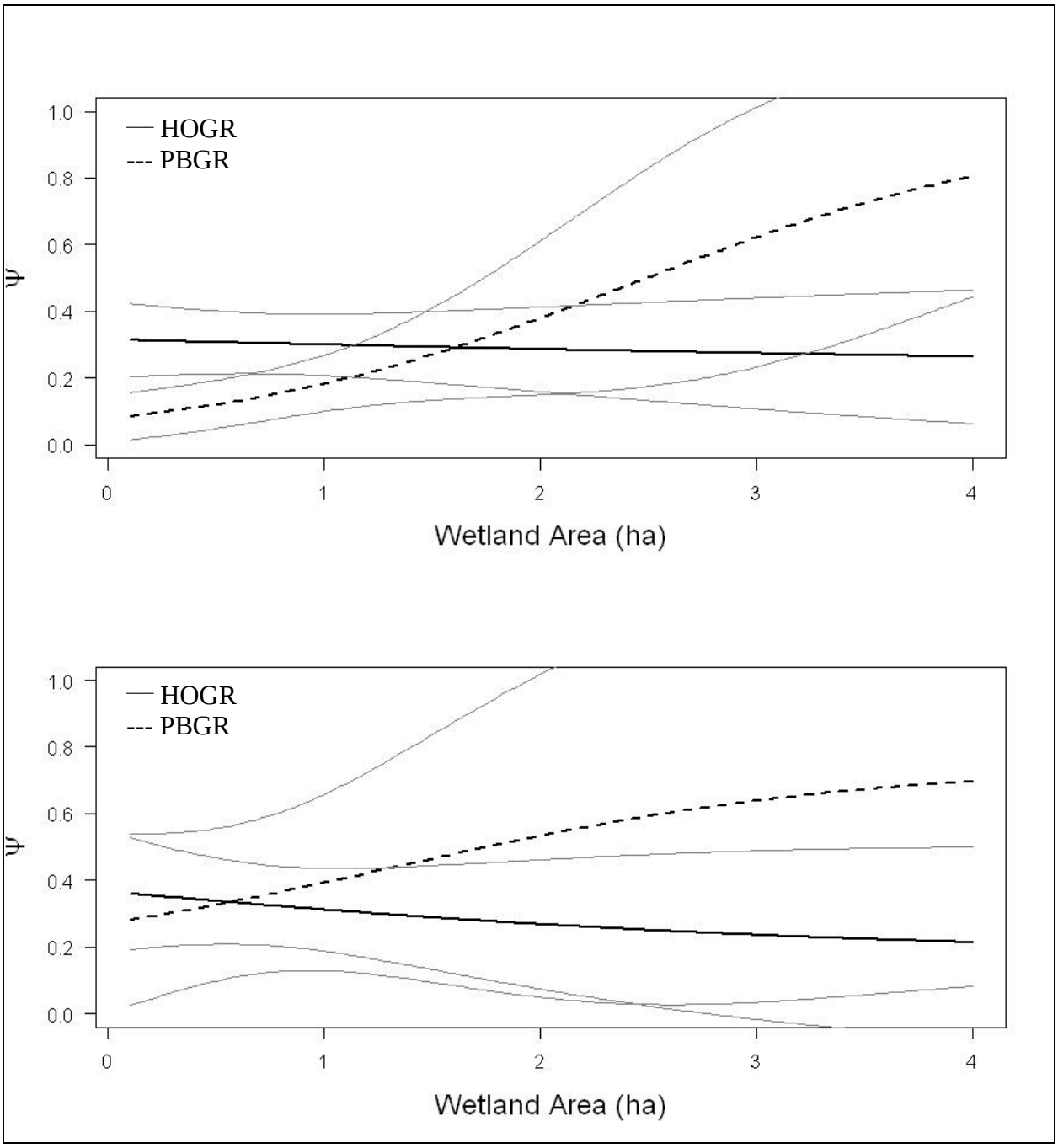


**Figure 3.18** Model-averaged occupancy probability prediction for breeding horned and pied-billed grebe adults (top) and broods (bottom) in relation to wetland area (Table 3.1) in 2010.

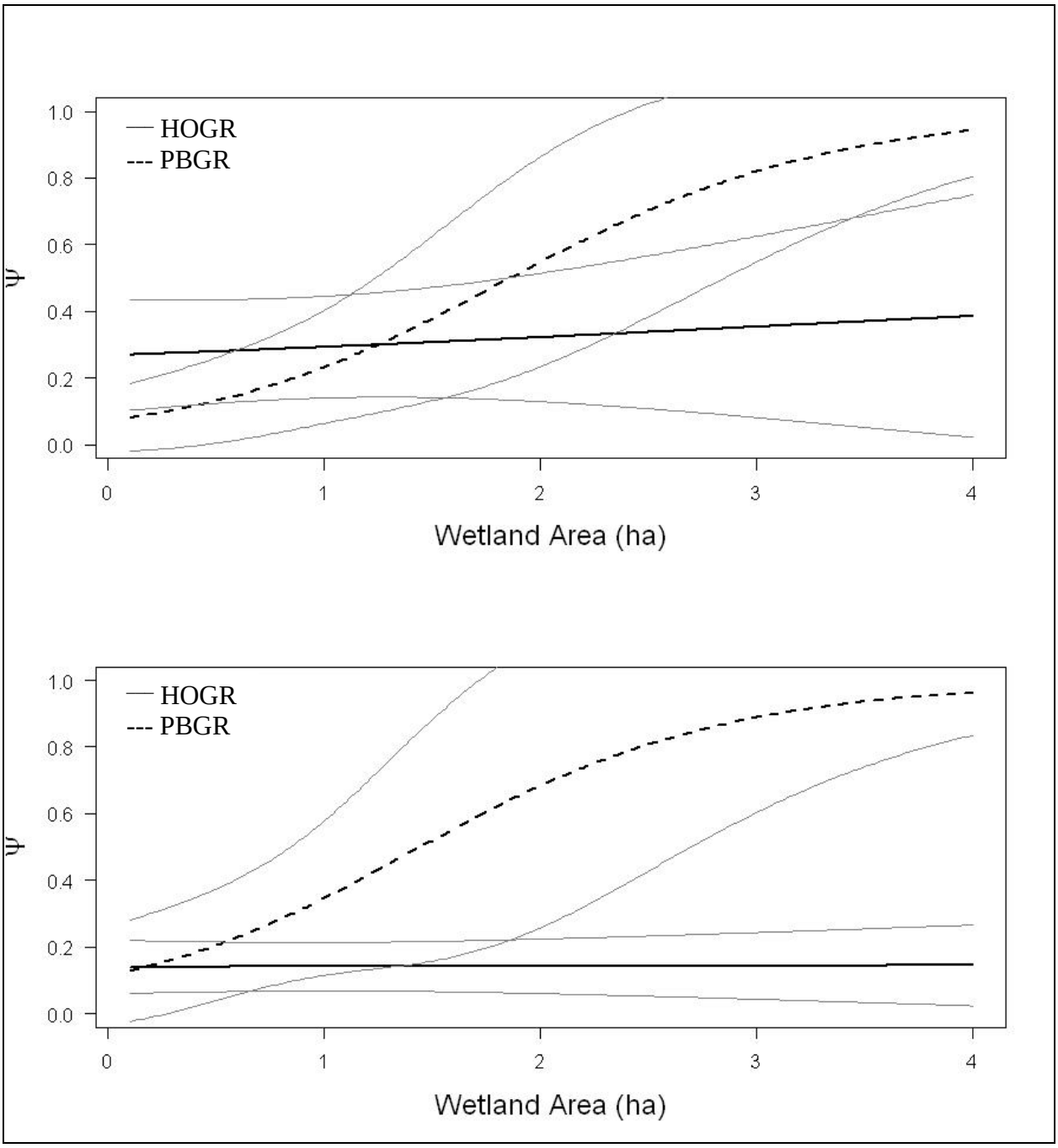


**Figure 3.19** Model-averaged occupancy probability prediction for breeding horned and pied-billed grebe adults (top) and broods (bottom) in relation to wetland area (Table 3.1) in 2011.

# CHAPTER 4. SYNTHESIS

In general, waterbirds are a relatively under-studied group of species whose basic biology is poorly known, thus compounding issues facing conservation initiatives. For example, little information exists regarding the status and trends of many waterbird species, including grebes, and factors influencing breeding distributions and productivity are not well understood. In this study, I sought to evaluate estimation methods for grebes while improving our understanding of the biological aspects of breeding habitat use along with patterns of productivity in prairie Canada. Obtaining unbiased relative abundance estimates is critical for determining the status and trend of populations which are then used to guide management objectives required to achieve conservation goals. The combination of cryptic behaviour of many waterbird species and the fact that they often breed in densely-vegetated habitats means that obtaining unbiased population estimates requires accounting for imperfect detection.

In Chapter 2, I aimed to expand the scope of large-scale information acquisition for species of conservation concern. Conservation organizations are striving to provide broad-scale monitoring programs that provide information on the population trends of a wider range of avian species, including waterbirds. The ground component of the annual Waterfowl Breeding Population and Habitat Survey (WBPHS) is a prairie-wide monitoring framework that could be modified for monitoring horned grebe populations without adding significant financial and logistical costs. Despite this, I suspect there are no other waterbird species that could be feasibly incorporated into the WBPHS without making considerable changes to current survey protocols due to, for example, their cryptic, nocturnal, or colonial behaviours.

In addition to the numerous financial and logistical issues facing waterbird monitoring programs, managers must weigh the value of quantifying habitat associations versus long-term

status and trend assessment. Although the latter certainly has its utility in determining whether or not populations are in decline, the data are often unavailable or too expensive to collect and they do not provide insight into why declines are occurring. As a result, fine-scale studies are needed to identify critical habitat and demographic issues which can then be projected to larger spatial scales which, in the end, may prove more profitable. Here, I have examined the practicality of including grebes in the WBPHS to provide annual measures of abundance while also providing insight into the factors influencing the distribution and productivity of grebes.

In Chapter 3, I examined the factors and processes involved in grebe habitat selection that operate at varying, hierarchical scales. In general, waterbird research has aimed to identify wetland specific habitat factors that contribute to breeding habitat selection but has generally failed to consider the influence of habitat heterogeneity at broader landscape level scales. Similarly, relatively few studies have considered what factors and processes that typify productive habitats. Here, I considered several processes and factors affecting breeding habitat selection at a wider range of scales, as well as the implications for subsequent productivity. Breeding pied-billed and horned grebes select wetlands that will persist throughout the summer to provide ample time for their young to fledge. Thus, breeding grebes avoid seasonal wetlands and rely almost exclusively on semi-permanent, permanent, and artificial wetlands.

Grebes are highly territorial species and rarely co-occur intra- and inter-specifically on wetlands <4ha. As a result, grebes have developed contrasting habitat preferences that enable them to coexist inter-specifically by taking advantage of wetland heterogeneity (Nudds 1982). Despite this, competitive interactions do occur on wetlands where preferred wetland characteristics for both species overlap. For example, breeding horned grebes select wetlands with 0-20% emergent vegetation to open water whereas pied-billed grebes preferred wetlands

with 20-40% emergent vegetation to open water. Thus, in most cases differential habitat preferences will prevent interspecific competition, but we expect competitive interaction to increase on wetlands with approximately 20% emergent vegetation to open water (where habitat preferences overlap). In general, breeding grebes selected habitats within landscapes composed of higher densities of semi-permanent, permanent, and artificial wetlands. This suggests that breeding adults select wetlands based on wetland specific factors as well as landscape composition. However, since high wetland density landscapes contain more available habitat, these areas contribute more to overall annual production.

In general, the wetland-specific habitat factors that influenced habitat selection by adults also strongly predicted brood occupancy probability. Broods are more likely to occur in high wetland density landscapes which further suggest that these landscapes are critical in the annual production of young.

## 4.1 Management implications and future research

As described above, my broad goal was to provide new insights regarding habitat associations and productivity relationships of horned and pied-billed grebes, information that can be used to project management programs and policy initiatives throughout the Canadian PPR. For example, understanding the factors that influence breeding grebe occupancy probability can be used in conjunction with geographic information systems to create spatially explicit maps (also know as “thunderstorm” maps) used in identifying critical habitat areas for conservation initiatives. This research has also shown that densities of breeding adults are indeed indicative of brood densities. Thus, efforts that target the counting of breeding adults can also be used to infer overall production potential.

Conservation organizations are striving to provide broad-scale monitoring programs that provide information on the population trends of a wider range of avian species, including waterbirds. I have shown that the ground component of the WBPHS can provide a monitoring framework that could be modified for monitoring annual variation in horned grebe populations without adding significant financial and logistical costs. Should these practices be conduced over many years, this may provide a source of information on long-term trend analysis of horned grebes. Additionally, expanding these methods to include Alberta and Manitoba WBPHS ground crew areas would provide broader-scale monitoring of grebe distributions and relative abundances over time.

Incorporating horned grebes in the WBPHS ground crew surveys would yield much-needed population estimates (COSEWIC 2009). The primary expenses for any avian monitoring program are those associated with collecting data across vast expanses of habitat (e.g., wages, transportation, and accommodations). Since the WBPHS ground component is a pre-existing large-scale operation, the inclusion of horned grebes may be financially and logistically feasible compared to alternative survey methods.

Because the detection probabilities of horned grebes on the WBPHS ground crew surveys are relatively high and consistent, relative abundance may be used as a population index to monitor annual and spatial variation in abundances provided that all grebe observations are recorded. Results of this investigation suggest that pied-billed grebe monitoring cannot be efficiently implemented into the current WBPHS ground crew survey protocol without substantially increasing the number of wetlands sampled with a grebe call-broadcast protocol. Conservation initiatives concerned with the population status and trend of pied-billed grebes should consider other means of monitoring such as Bird Studies Canada's Prairie and Parkland

Marshbird Monitoring Program (Bird Studies Canada 2012). While there are advantages of conducting roadside surveys of grebes (e.g., to increase speed and scale of sampling), there may be drawbacks. For example, wetland densities and species-specific wetland use along roads may not be representative of the larger landscape (Austin et al. 2000). Since the WBPHS ground segments are centered on roads, examining how grebe breeding densities vary in relation to roads should be a priority.

Future research into the drivers of habitat segregation between grebe species is needed, particularly with respect to diets of adults and young. To properly address the conservation concerns of grebes, particularly those of horned grebes, accounting for threats to wintering grounds is of particular importance. For example, this species over-winters predominantly in the Gulf Coast which, in 2010, was subject to one of the largest marine oil spills ever; population impacts of this spill are unknown. Perhaps the most critical aspect of grebe breeding biology that is in need of research is the drivers of adult survival and reproductive success. I have shown how overall population productivity can be influenced by competition and habitat selection at varying scales, however, the factors and processes that influence the fitness of breeding grebes remain unclear.

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# APPENDIX A

The following is the grebe survey protocol used in this study.

Grebe Survey

1) Weather conditions will be collected at the outset of each survey day: temperature, wind speed, percent cloud cover, precipitation, and direction facing for the survey. Weather criteria for conducting the surveys will remain the same as the WBPHS (USFWS and CWS 1987).
2) Surveyors will independently observe ponds at a distance of 0-50 m (buffer) and record all grebes detected (note, by sight or sound) in EACH of 4 time intervals using the following methods:
    a. minute 0-1: silent observation*
    b. minute 1-2: horned grebe call
    c. minute 2-3: pied-billed grebe call
    d. minute 3-4: final silent observation.

Habitat Characterization

Habitat attributes to be collected include:

1) Pond type.
2) Wetland location using GPS and wetland area (one time only during the breeding season)
3) Percent of (in 20% increments; totalling 100%):
    a. emergent cover;
    b. open water/floating vegetation;
    c. shrubs/ trees; or

d. exposed mud, rocks, sand or other substrate materials.

4) Dominant emergent vegetation types (in 20% increments; totalling 100%; no woody vegetation types):

    a. cattail;

    b. sedge;

    c. rush/spike rush;

    d. grass species.; or

    e. other.

5) Upland type and percent impacts to 100 m outside the outer margin edges:

    a. intensive farming;

    b. grasslands and haylands;

    c. grazed; or

    d. wooded.

* During the WBPHS, if a large wetland with numerous birds takes >1 minute to document all observed waterbirds, immediately begin the second minute after the first completed count.

## APPENDIX B

Table B1. Summary of cumulative model weights ($\sum$ AIC$w_i$) for the detection probability ($p$) of breeding adult horned and pied-billed grebes and broods in the Canadian PPR in 2010 and 2011(i.e., calculated by summing the AIC weight [$w_i$] for all models containing a specific variable). See text for a description of all variables.

| | ADULTS | | | | BROODS | | | |
|---|---|---|---|---|---|---|---|---|
| | HOGR | | PBGR | | HOGR | | PBGR | |
| Variable | 2010 | 2011 | 2010 | 2011 | 2010 | 2011 | 2010 | 2011 |
| Date | 0.28 | 0.29 | 0.30 | 0.26 | 0.30 | 0.25 | 0.35 | 0.78 |
| Temp | 0.26 | 0.37 | 0.35 | 0.29 | 0.37 | 0.34 | 0.28 | 0.32 |
| Cloud cover | 0.27 | 0.28 | 0.29 | 0.26 | 0.52 | 0.32 | 0.26 | 0.36 |
| Wind | 0.34 | 0.38 | 0.26 | 0.30 | 0.38 | 0.36 | 0.30 | 0.63 |
| Time | 0.43 | 0.26 | 0.71 | 0.34 | 0.27 | 0.27 | 0.25 | 0.32 |

## APPENDIX C

Table C1. Summary of the entire candidate model set (including additive and interaction terms) ranked by AIC with the best-approximating model at the top for breeding horned grebe occupancy probability (ψ) with constant detection probability *p*(.), Saskatchewan, 2010. Variable names used in models are defined in Table 3.1.

| Model[a] | AIC[a] | ΔAIC[b] | $w_i$[c] | $K$[d] | Model[a] |
|---|---|---|---|---|---|
| ψ(HTSP+EVOW+LAND) | 246.83 | 0.00 | 0.13 | 0.13 | 5 |
| ψ(HTSP+LAND) | 247.46 | 0.63 | 0.10 | 0.23 | 4 |
| ψ(HTSP+EVOW) | 247.62 | 0.79 | 0.09 | 0.32 | 4 |
| ψ(EVOW+LAND) | 248.49 | 1.66 | 0.06 | 0.38 | 4 |
| ψ(HTSP+AREA+EVOW+LAND) | 248.59 | 1.76 | 0.06 | 0.44 | 6 |
| ψ(EVOW) | 248.59 | 1.77 | 0.06 | 0.49 | 3 |
| ψ(HTSP+EVOW+EVOW2+LAND) | 248.78 | 1.95 | 0.05 | 0.54 | 6 |
| ψ(HTSP) | 248.90 | 2.08 | 0.05 | 0.59 | 3 |
| ψ(HTSP+AREA+LAND) | 249.17 | 2.34 | 0.04 | 0.63 | 5 |
| ψ(AREA+EVOW+LAND) | 249.46 | 2.63 | 0.04 | 0.67 | 5 |
| ψ(HTSP+AREA+EVOW) | 249.50 | 2.67 | 0.04 | 0.70 | 5 |
| ψ(HTSP+EVOW+EVOW2) | 249.62 | 2.79 | 0.03 | 0.74 | 5 |
| ψ(LAND) | 249.81 | 2.98 | 0.03 | 0.77 | 3 |
| ψ(AREA+EVOW) | 249.90 | 3.07 | 0.03 | 0.80 | 4 |
| ψ(.) | 250.24 | 3.41 | 0.02 | 0.82 | 2 |
| ψ(EVOW+EVOW2+LAND) | 250.38 | 3.55 | 0.02 | 0.84 | 5 |
| ψ(HTSP+AREA+EVOW+EVOW2+LAND) | 250.57 | 3.74 | 0.02 | 0.86 | 7 |

| | | | | | |
|---|---|---|---|---|---|
| ψ(EVOW+EVOW2) | 250.58 | 3.75 | 0.02 | 0.88 | 4 |
| ψ(AREA+LAND) | 250.59 | 3.76 | 0.02 | 0.90 | 4 |
| ψ(HTSP+AREA) | 250.76 | 3.93 | 0.02 | 0.92 | 4 |
| ψ(AREA+EVOW+EVOW2+LAND) | 251.43 | 4.60 | 0.01 | 0.94 | 6 |
| ψ(AREA) | 251.43 | 4.61 | 0.01 | 0.95 | 3 |
| ψ(HTSP+AREA+EVOW+EVOW2) | 251.49 | 4.66 | 0.01 | 0.96 | 6 |
| ψ(AREA+EVOW+EVOW2) | 251.90 | 5.07 | 0.01 | 0.97 | 5 |
| ψ(HTSP+AREA*EVOW+EVOW2+LAND) | 252.03 | 5.20 | 0.01 | 0.98 | 8 |
| ψ(AREA*EVOW+EVOW2+LAND) | 252.95 | 6.13 | 0.01 | 0.99 | 7 |
| ψ(HTSP+AREA*EVOW+EVOW2) | 253.14 | 6.31 | 0.01 | 1.00 | 7 |
| ψ(AREA*EVOW+EVOW2) | 253.52 | 6.70 | 0.00 | 1.00 | 6 |

[a] Models are denoted as additive (+) and/or multiplicative (*); Variables are defined in Table 3.1.

[b] Akaike's Information Criterion.

[c] Difference in AICc relative to smallest value.

[d] Akaike's weight of models.

[e] Number of parameters.

Table C2. Summary of the entire candidate model set (including additive and interaction terms) ranked by AIC with the best-approximating model at the top for breeding horned grebe occupancy probability (ψ) with constant detection probability *p*(.), Saskatchewan, 2011. Variable names used in models are defined in Table 3.1.

| Model[a] | AIC[a] | ΔAIC[b] | $w_i$[c] | $K$[d] | Model[a] |
|---|---|---|---|---|---|
| ψ(HTSP+EVOW+EVOW2+LAND) | 201.70 | 0.00 | 0.24 | 0.24 | 6 |
| ψ(HTSP+AREA+EVOW+EVOW2+LAND) | 202.63 | 0.93 | 0.15 | 0.40 | 7 |
| ψ(HTSP+EVOW+LAND) | 202.97 | 1.27 | 0.13 | 0.52 | 5 |
| ψ(HTSP+AREA*EVOW+EVOW2+LAND) | 203.16 | 1.46 | 0.12 | 0.64 | 8 |
| ψ(HTSP+AREA+EVOW+LAND) | 203.93 | 2.23 | 0.08 | 0.72 | 6 |
| ψ(HTSP+AREA+EVOW+EVOW2) | 205.06 | 3.36 | 0.05 | 0.77 | 6 |
| ψ(EVOW+LAND) | 205.21 | 3.52 | 0.04 | 0.81 | 4 |
| ψ(EVOW+EVOW2+LAND) | 205.24 | 3.54 | 0.04 | 0.85 | 5 |
| ψ(AREA*EVOW+EVOW2+LAND) | 205.62 | 3.92 | 0.03 | 0.88 | 7 |
| ψ(HTSP+EVOW+EVOW2) | 205.91 | 4.21 | 0.03 | 0.91 | 5 |
| ψ(HTSP+AREA*EVOW+EVOW2) | 206.27 | 4.58 | 0.02 | 0.94 | 7 |
| ψ(AREA+EVOW+LAND) | 207.12 | 5.43 | 0.02 | 0.96 | 5 |
| ψ(AREA+EVOW+EVOW2+LAND) | 207.20 | 5.51 | 0.02 | 0.97 | 6 |
| ψ(HTSP+AREA+EVOW) | 207.56 | 5.86 | 0.01 | 0.98 | 5 |
| ψ(HTSP+EVOW) | 208.45 | 6.76 | 0.01 | 0.99 | 4 |
| ψ(EVOW+EVOW2) | 210.95 | 9.25 | 0.00 | 0.99 | 4 |
| ψ(AREA*EVOW+EVOW2) | 211.52 | 9.83 | 0.00 | 1.00 | 6 |

| | | | | | |
|---|---|---|---|---|---|
| ψ(EVOW) | 211.57 | 9.88 | 0.00 | 1.00 | 3 |
| ψ(AREA+EVOW+EVOW2) | 212.40 | 10.70 | 0.00 | 1.00 | 5 |
| ψ(AREA+EVOW) | 212.78 | 11.08 | 0.00 | 1.00 | 4 |
| ψ(HTSP+AREA) | 219.86 | 18.16 | 0.00 | 1.00 | 4 |
| ψ(HTSP+AREA+LAND) | 220.52 | 18.83 | 0.00 | 1.00 | 5 |
| ψ(HTSP+LAND) | 221.30 | 19.60 | 0.00 | 1.00 | 4 |
| ψ(HTSP) | 221.96 | 20.27 | 0.00 | 1.00 | 3 |
| ψ(LAND) | 225.13 | 23.43 | 0.00 | 1.00 | 3 |
| ψ(.) | 226.20 | 24.50 | 0.00 | 1.00 | 2 |
| ψ(AREA+LAND) | 226.59 | 24.90 | 0.00 | 1.00 | 4 |
| ψ(AREA) | 227.03 | 25.34 | 0.00 | 1.00 | 3 |

[a] Models are denoted as additive (+) and/or multiplicative (*); Variables are defined in Table 3.1.

[b] Akaike's Information Criterion.

[c] Difference in AICc relative to smallest value.

[d] Akaike's weight of models.

[e] Number of parameters.

Table C3. Summary of the entire candidate model set (including additive and interaction terms) ranked by AIC with the best-approximating model at the top for horned grebe brood occupancy probability (ψ) with constant detection probability *p*(.), Saskatchewan, 2010. Variable names used in models are defined in Table 3.1.

| Model[a] | AIC[a] | ΔAIC[b] | $w_i$[c] | $K$[d] | Model[a] |
|---|---|---|---|---|---|
| ψ(HTSP+LAND) | 255.27 | 0.00 | 0.24 | 0.24 | 4 |
| ψ(HTSP+AREA+LAND) | 255.72 | 0.45 | 0.20 | 0.44 | 5 |
| ψ(HTSP+EVOW+LAND) | 257.27 | 2.00 | 0.09 | 0.53 | 5 |
| ψ(HTSP) | 257.51 | 2.24 | 0.08 | 0.61 | 3 |
| ψ(HTSP+AREA+EVOW+LAND) | 257.72 | 2.45 | 0.07 | 0.68 | 6 |
| ψ(HTSP+AREA) | 258.11 | 2.84 | 0.06 | 0.74 | 4 |
| ψ(HTSP+EVOW+EVOW2+LAND) | 258.65 | 3.38 | 0.05 | 0.79 | 6 |
| ψ(HTSP+AREA+EVOW+EVOW2+LAND) | 259.29 | 4.03 | 0.03 | 0.82 | 7 |
| ψ(HTSP+EVOW) | 259.37 | 4.11 | 0.03 | 0.85 | 4 |
| ψ(HTSP+AREA+EVOW) | 259.90 | 4.64 | 0.02 | 0.87 | 5 |
| ψ(AREA+LAND) | 260.63 | 5.37 | 0.02 | 0.89 | 4 |
| ψ(AREA) | 260.95 | 5.68 | 0.01 | 0.90 | 3 |
| ψ(HTSP+AREA*EVOW+EVOW2+LAND) | 261.08 | 5.82 | 0.01 | 0.92 | 8 |
| ψ(HTSP+EVOW+EVOW2) | 261.25 | 5.98 | 0.01 | 0.93 | 5 |
| ψ(.) | 261.57 | 6.31 | 0.01 | 0.94 | 2 |
| ψ(LAND) | 261.68 | 6.41 | 0.01 | 0.95 | 3 |
| ψ(HTSP+AREA+EVOW+EVOW2) | 261.85 | 6.59 | 0.01 | 0.96 | 6 |

| | | | | | |
|---|---|---|---|---|---|
| ψ(AREA+EVOW+LAND) | 262.46 | 7.20 | 0.01 | 0.97 | 5 |
| ψ(AREA+EVOW) | 262.56 | 7.29 | 0.01 | 0.97 | 4 |
| ψ(EVOW) | 263.26 | 8.00 | 0.00 | 0.98 | 3 |
| ψ(AREA+EVOW+EVOW2+LAND) | 263.46 | 8.20 | 0.00 | 0.98 | 6 |
| ψ(EVOW+LAND) | 263.53 | 8.26 | 0.00 | 0.99 | 4 |
| ψ(HTSP+AREA*EVOW+EVOW2) | 263.74 | 8.47 | 0.00 | 0.99 | 7 |
| ψ(EVOW+EVOW2+LAND) | 263.98 | 8.71 | 0.00 | 0.99 | 5 |
| ψ(AREA+EVOW+EVOW2) | 264.20 | 8.93 | 0.00 | 1.00 | 5 |
| ψ(EVOW+EVOW2) | 264.54 | 9.27 | 0.00 | 1.00 | 4 |
| ψ(AREA*EVOW+EVOW2+LAND) | 265.45 | 10.19 | 0.00 | 1.00 | 7 |
| ψ(AREA*EVOW+EVOW2) | 266.19 | 10.93 | 0.00 | 1.00 | 6 |

[a] Models are denoted as additive (+) and/or multiplicative (*); Variables are defined in Table 3.1.

[b] Akaike's Information Criterion.

[c] Difference in AICc relative to smallest value.

[d] Akaike's weight of models.

[e] Number of parameters.

Table C4. Summary of the entire candidate model set (including additive and interaction terms) ranked by AIC with the best-approximating model at the top for horned grebe brood occupancy probability (ψ) with constant detection probability *p*(.), Saskatchewan, 2011. Variable names used in models are defined in Table 3.1.

| Model[a] | AIC[a] | ΔAIC[b] | $w_i$[c] | $K$[d] | Model[a] |
|---|---|---|---|---|---|
| ψ(EVOW+LAND) | 157.79 | 0.00 | 0.19 | 0.19 | 4 |
| ψ(HTSP+EVOW+LAND) | 158.66 | 0.86 | 0.12 | 0.32 | 5 |
| ψ(HTSP+EVOW) | 159.61 | 1.82 | 0.08 | 0.39 | 4 |
| ψ(EVOW) | 159.67 | 1.88 | 0.07 | 0.47 | 3 |
| ψ(AREA+EVOW+LAND) | 159.76 | 1.96 | 0.07 | 0.54 | 5 |
| ψ(EVOW+EVOW2+LAND) | 159.79 | 2.00 | 0.07 | 0.61 | 5 |
| ψ(HTSP+EVOW+EVOW2+LAND) | 160.62 | 2.83 | 0.05 | 0.66 | 6 |
| ψ(HTSP+AREA+EVOW+LAND) | 160.65 | 2.86 | 0.05 | 0.70 | 6 |
| ψ(HTSP+AREA+EVOW) | 161.32 | 3.53 | 0.03 | 0.74 | 5 |
| ψ(HTSP+EVOW+EVOW2) | 161.53 | 3.73 | 0.03 | 0.77 | 5 |
| ψ(AREA+EVOW) | 161.64 | 3.84 | 0.03 | 0.79 | 4 |
| ψ(EVOW+EVOW2) | 161.67 | 3.87 | 0.03 | 0.82 | 4 |
| ψ(AREA+EVOW+EVOW2+LAND) | 161.76 | 3.96 | 0.03 | 0.85 | 6 |
| ψ(HTSP+AREA+EVOW+EVOW2+LAND) | 162.62 | 4.82 | 0.02 | 0.86 | 7 |
| ψ(LAND) | 162.64 | 4.84 | 0.02 | 0.88 | 3 |
| ψ(.) | 162.72 | 4.93 | 0.02 | 0.90 | 2 |
| ψ(HTSP) | 163.05 | 5.25 | 0.01 | 0.91 | 3 |

| | | | | | |
|---|---|---|---|---|---|
| ψ(HTSP+AREA+EVOW+EVOW2) | 163.24 | 5.44 | 0.01 | 0.92 | 6 |
| ψ(AREA*EVOW+EVOW2+LAND) | 163.37 | 5.57 | 0.01 | 0.94 | 7 |
| ψ(HTSP+LAND) | 163.49 | 5.70 | 0.01 | 0.95 | 4 |
| ψ(AREA+EVOW+EVOW2) | 163.63 | 5.84 | 0.01 | 0.96 | 5 |
| ψ(HTSP+AREA*EVOW+EVOW2+LAND) | 164.00 | 6.21 | 0.01 | 0.97 | 8 |
| ψ(HTSP+AREA*EVOW+EVOW2) | 164.59 | 6.79 | 0.01 | 0.97 | 7 |
| ψ(AREA+LAND) | 164.63 | 6.83 | 0.01 | 0.98 | 4 |
| ψ(HTSP+AREA) | 164.67 | 6.87 | 0.01 | 0.99 | 4 |
| ψ(AREA) | 164.68 | 6.88 | 0.01 | 0.99 | 3 |
| ψ(AREA*EVOW+EVOW2) | 165.25 | 7.45 | 0.00 | 1.00 | 6 |
| ψ(HTSP+AREA+LAND) | 165.42 | 7.62 | 0.00 | 1.00 | 5 |

[a] Models are denoted as additive (+) and/or multiplicative (*); Variables are defined in Table 3.1.

[b] Akaike's Information Criterion.

[c] Difference in AICc relative to smallest value.

[d] Akaike's weight of models.

[e] Number of parameters.

Table C5. Summary of the entire candidate model set (including additive and interaction terms) ranked by AIC with the best-approximating model at the top for breeding pied-billed grebe occupancy probability (ψ) with constant detection probability *p*(.), Saskatchewan, 2010. Variable names used in models are defined in Table 3.1.

| Model[a] | AIC[a] | ΔAIC[b] | $w_i$[c] | $K$[d] | Model[a] |
|---|---|---|---|---|---|
| ψ(HTSP+AREA+LAND) | 171.43 | 0.00 | 0.18 | 0.18 | 5 |
| ψ(HTSP+AREA) | 171.78 | 0.35 | 0.15 | 0.33 | 4 |
| ψ(AREA) | 172.25 | 0.82 | 0.12 | 0.45 | 3 |
| ψ(AREA+LAND) | 172.30 | 0.88 | 0.12 | 0.57 | 4 |
| ψ(HTSP+AREA+EVOW+LAND) | 173.08 | 1.65 | 0.08 | 0.65 | 6 |
| ψ(HTSP+AREA+EVOW) | 173.54 | 2.11 | 0.06 | 0.71 | 5 |
| ψ(AREA+EVOW+LAND) | 173.62 | 2.20 | 0.06 | 0.77 | 5 |
| ψ(AREA+EVOW) | 173.77 | 2.34 | 0.06 | 0.83 | 4 |
| ψ(HTSP+AREA+EVOW+EVOW2+LAND) | 175.06 | 3.63 | 0.03 | 0.86 | 7 |
| ψ(HTSP+AREA+EVOW+EVOW2) | 175.51 | 4.09 | 0.02 | 0.88 | 6 |
| ψ(AREA+EVOW+EVOW2+LAND) | 175.60 | 4.18 | 0.02 | 0.90 | 6 |
| ψ(AREA+EVOW+EVOW2) | 175.74 | 4.32 | 0.02 | 0.92 | 5 |
| ψ(HTSP+LAND) | 176.79 | 5.36 | 0.01 | 0.94 | 4 |
| ψ(HTSP+AREA*EVOW+EVOW2+LAND) | 177.05 | 5.62 | 0.01 | 0.95 | 8 |
| ψ(HTSP+AREA*EVOW+EVOW2) | 177.43 | 6.01 | 0.01 | 0.96 | 7 |
| ψ(AREA*EVOW+EVOW2+LAND) | 177.60 | 6.18 | 0.01 | 0.96 | 7 |
| ψ(AREA*EVOW+EVOW2) | 177.71 | 6.29 | 0.01 | 0.97 | 6 |

| | | | | | |
|---|---|---|---|---|---|
| ψ(HTSP) | 178.28 | 6.86 | 0.01 | 0.98 | 3 |
| ψ(HTSP+EVOW+LAND) | 178.55 | 7.12 | 0.01 | 0.98 | 5 |
| ψ(LAND) | 179.13 | 7.70 | 0.00 | 0.99 | 3 |
| ψ(.) | 179.62 | 8.19 | 0.00 | 0.99 | 2 |
| ψ(HTSP+EVOW) | 180.16 | 8.73 | 0.00 | 0.99 | 4 |
| ψ(HTSP+EVOW+EVOW2+LAND) | 180.37 | 8.94 | 0.00 | 0.99 | 6 |
| ψ(EVOW+LAND) | 180.48 | 9.05 | 0.00 | 1.00 | 4 |
| ψ(EVOW) | 181.20 | 9.78 | 0.00 | 1.00 | 3 |
| ψ(HTSP+EVOW+EVOW2) | 181.76 | 10.33 | 0.00 | 1.00 | 5 |
| ψ(EVOW+EVOW2+LAND) | 182.21 | 10.79 | 0.00 | 1.00 | 5 |
| ψ(EVOW+EVOW2) | 182.74 | 11.31 | 0.00 | 1.00 | 4 |

[a] Models are denoted as additive (+) and/or multiplicative (*); Variables are defined in Table 3.1.

[b] Akaike's Information Criterion.

[c] Difference in AICc relative to smallest value.

[d] Akaike's weight of models.

[e] Number of parameters.

Table C6. Summary of the entire candidate model set (including additive and interaction terms) ranked by AIC with the best-approximating model at the top for breeding pied-billed grebe occupancy probability (ψ) with constant detection probability *p*(.), Saskatchewan, 2011. Variable names used in models are defined in Table 3.1.

| Model[a] | AIC[a] | ΔAIC[b] | $w_i$[c] | $K$[d] | Model[a] |
|---|---|---|---|---|---|
| ψ(AREA*EVOW+EVOW2+LAND) | 148.72 | 0.00 | 0.33 | 0.33 | 7 |
| ψ(HTSP+AREA*EVOW+EVOW2) | 149.39 | 0.67 | 0.23 | 0.56 | 7 |
| ψ(HTSP+AREA*EVOW+EVOW2+LAND) | 149.40 | 0.68 | 0.23 | 0.79 | 8 |
| ψ(AREA*EVOW+EVOW2) | 150.81 | 2.09 | 0.11 | 0.91 | 6 |
| ψ(AREA+EVOW+EVOW2+LAND) | 153.65 | 4.92 | 0.03 | 0.93 | 6 |
| ψ(HTSP+AREA+EVOW+EVOW2+LAND) | 154.16 | 5.44 | 0.02 | 0.95 | 7 |
| ψ(HTSP+AREA+EVOW+EVOW2) | 154.82 | 6.10 | 0.02 | 0.97 | 6 |
| ψ(AREA+EVOW+EVOW2) | 155.75 | 7.02 | 0.01 | 0.98 | 5 |
| ψ(HTSP+AREA) | 156.93 | 8.21 | 0.01 | 0.99 | 4 |
| ψ(HTSP+AREA+LAND) | 157.80 | 9.07 | 0.00 | 0.99 | 5 |
| ψ(AREA) | 158.46 | 9.74 | 0.00 | 0.99 | 3 |
| ψ(AREA+LAND) | 158.66 | 9.94 | 0.00 | 0.99 | 4 |
| ψ(HTSP+AREA+EVOW) | 158.72 | 10.00 | 0.00 | 1.00 | 5 |
| ψ(HTSP+AREA+EVOW+LAND) | 159.10 | 10.38 | 0.00 | 1.00 | 6 |
| ψ(AREA+EVOW+LAND) | 159.56 | 10.84 | 0.00 | 1.00 | 5 |
| ψ(AREA+EVOW) | 160.12 | 11.40 | 0.00 | 1.00 | 4 |
| ψ(HTSP+EVOW+EVOW2) | 166.87 | 18.15 | 0.00 | 1.00 | 5 |

| | | | | | |
|---|---|---|---|---|---|
| ψ(EVOW+EVOW2) | 167.73 | 19.01 | 0.00 | 1.00 | 4 |
| ψ(HTSP+EVOW+EVOW2+LAND) | 168.77 | 20.05 | 0.00 | 1.00 | 6 |
| ψ(EVOW+EVOW2+LAND) | 169.19 | 20.47 | 0.00 | 1.00 | 5 |
| ψ(HTSP) | 171.72 | 23.00 | 0.00 | 1.00 | 3 |
| ψ(.) | 172.87 | 24.15 | 0.00 | 1.00 | 2 |
| ψ(HTSP+LAND) | 173.71 | 24.99 | 0.00 | 1.00 | 4 |
| ψ(HTSP+EVOW) | 173.72 | 25.00 | 0.00 | 1.00 | 4 |
| ψ(EVOW) | 174.66 | 25.94 | 0.00 | 1.00 | 3 |
| ψ(LAND) | 174.76 | 26.04 | 0.00 | 1.00 | 3 |
| ψ(HTSP+EVOW+LAND) | 175.71 | 26.99 | 0.00 | 1.00 | 5 |
| ψ(EVOW+LAND) | 176.46 | 27.74 | 0.00 | 1.00 | 4 |

[a] Models are denoted as additive (+) and/or multiplicative (*); Variables are defined in Table 3.1.

[b] Akaike's Information Criterion.

[c] Difference in AICc relative to smallest value.

[d] Akaike's weight of models.

[e] Number of parameters.

Table C7. Summary of the entire candidate model set (including additive and interaction terms) ranked by AIC with the best-approximating model at the top for pied-billed grebe brood occupancy probability (ψ) with constant detection probability *p*(.), Saskatchewan, 2010. Variable names used in models are defined in Table 3.1.

| Model[a] | AIC[a] | ΔAIC[b] | $w_i$[c] | $K$[d] | Model[a] |
|---|---|---|---|---|---|
| ψ(HTSP+AREA+LAND) | 210.63 | 0.00 | 0.18 | 0.18 | 5 |
| ψ(HTSP+LAND) | 211.30 | 0.67 | 0.13 | 0.31 | 4 |
| ψ(HTSP+AREA+EVOW+LAND) | 211.52 | 0.89 | 0.12 | 0.42 | 6 |
| ψ(HTSP+AREA+EVOW+EVOW2+LAND) | 211.64 | 1.01 | 0.11 | 0.53 | 7 |
| ψ(HTSP+AREA*EVOW+EVOW2+LAND) | 211.76 | 1.13 | 0.10 | 0.63 | 8 |
| ψ(HTSP+EVOW+EVOW2+LAND) | 211.93 | 1.29 | 0.09 | 0.73 | 6 |
| ψ(HTSP+EVOW+LAND) | 212.39 | 1.76 | 0.07 | 0.80 | 5 |
| ψ(AREA+LAND) | 214.02 | 3.39 | 0.03 | 0.84 | 4 |
| ψ(AREA+EVOW+EVOW2+LAND) | 214.30 | 3.67 | 0.03 | 0.86 | 6 |
| ψ(AREA+EVOW+LAND) | 214.52 | 3.89 | 0.03 | 0.89 | 5 |
| ψ(AREA*EVOW+EVOW2+LAND) | 215.19 | 4.56 | 0.02 | 0.91 | 7 |
| ψ(EVOW+EVOW2+LAND) | 215.75 | 5.11 | 0.01 | 0.92 | 5 |
| ψ(HTSP+AREA*EVOW+EVOW2) | 215.87 | 5.23 | 0.01 | 0.94 | 7 |
| ψ(HTSP+AREA+EVOW+EVOW2) | 216.00 | 5.37 | 0.01 | 0.95 | 6 |
| ψ(LAND) | 216.55 | 5.92 | 0.01 | 0.96 | 3 |
| ψ(HTSP+EVOW+EVOW2) | 216.80 | 6.17 | 0.01 | 0.97 | 5 |
| ψ(HTSP+AREA) | 216.88 | 6.25 | 0.01 | 0.97 | 4 |

| | | | | | |
|---|---|---|---|---|---|
| ψ(EVOW+LAND) | 217.13 | 6.50 | 0.01 | 0.98 | 4 |
| ψ(AREA*EVOW+EVOW2) | 218.22 | 7.59 | 0.00 | 0.98 | 6 |
| ψ(AREA+EVOW+EVOW2) | 218.29 | 7.66 | 0.00 | 0.99 | 5 |
| ψ(HTSP+AREA+EVOW) | 218.34 | 7.71 | 0.00 | 0.99 | 5 |
| ψ(AREA) | 219.58 | 8.95 | 0.00 | 0.99 | 3 |
| ψ(HTSP) | 219.64 | 9.00 | 0.00 | 1.00 | 3 |
| ψ(EVOW+EVOW2) | 219.97 | 9.33 | 0.00 | 1.00 | 4 |
| ψ(HTSP+EVOW) | 220.81 | 10.18 | 0.00 | 1.00 | 4 |
| ψ(AREA+EVOW) | 220.94 | 10.31 | 0.00 | 1.00 | 4 |
| ψ(.) | 223.70 | 13.07 | 0.00 | 1.00 | 2 |
| ψ(EVOW) | 224.57 | 13.93 | 0.00 | 1.00 | 3 |

[a] Models are denoted as additive (+) and/or multiplicative (*); Variables are defined in Table 3.1.

[b] Akaike's Information Criterion.

[c] Difference in AICc relative to smallest value.

[d] Akaike's weight of models.

[e] Number of parameters.

Table C8. Summary of the entire candidate model set (including additive and interaction terms) ranked by AIC with the best-approximating model at the top for pied-billed grebe brood occupancy probability (ψ) with constant detection probability *p*(.), Saskatchewan, 2011. Variable names used in models are defined in Table 3.1.

| Model[a] | AIC[a] | ΔAIC[b] | $w_i$[c] | $K$[d] | Model[a] |
|---|---|---|---|---|---|
| ψ(AREA*EVOW+EVOW2+LAND) | 194.68 | 0.00 | 0.36 | 0.36 | 7 |
| ψ(HTSP+AREA*EVOW+EVOW2+LAND) | 195.55 | 0.87 | 0.23 | 0.59 | 8 |
| ψ(AREA+EVOW+EVOW2+LAND) | 196.34 | 1.66 | 0.16 | 0.75 | 6 |
| ψ(HTSP+AREA+EVOW+EVOW2+LAND) | 197.23 | 2.55 | 0.10 | 0.85 | 7 |
| ψ(HTSP+AREA*EVOW+EVOW2) | 199.77 | 5.09 | 0.03 | 0.88 | 7 |
| ψ(AREA*EVOW+EVOW2) | 199.79 | 5.11 | 0.03 | 0.90 | 6 |
| ψ(AREA+LAND) | 200.46 | 5.78 | 0.02 | 0.92 | 4 |
| ψ(AREA+EVOW+EVOW2) | 200.91 | 6.23 | 0.02 | 0.94 | 5 |
| ψ(HTSP+AREA+LAND) | 200.93 | 6.25 | 0.02 | 0.95 | 5 |
| ψ(HTSP+AREA+EVOW+EVOW2) | 200.96 | 6.28 | 0.02 | 0.97 | 6 |
| ψ(HTSP+AREA+EVOW+LAND) | 201.77 | 7.09 | 0.01 | 0.98 | 6 |
| ψ(AREA+EVOW+LAND) | 201.78 | 7.10 | 0.01 | 0.99 | 5 |
| ψ(HTSP+AREA+EVOW) | 204.86 | 10.18 | 0.00 | 0.99 | 5 |
| ψ(AREA+EVOW) | 205.67 | 10.99 | 0.00 | 0.99 | 4 |
| ψ(AREA) | 206.07 | 11.39 | 0.00 | 1.00 | 3 |
| ψ(HTSP+AREA) | 206.17 | 11.49 | 0.00 | 1.00 | 4 |
| ψ(EVOW+EVOW2+LAND) | 206.18 | 11.49 | 0.00 | 1.00 | 5 |

| | | | | | |
|---|---|---|---|---|---|
| ψ(HTSP+EVOW+EVOW2+LAND) | 207.01 | 12.33 | 0.00 | 1.00 | 6 |
| ψ(EVOW+EVOW2) | 207.44 | 12.76 | 0.00 | 1.00 | 4 |
| ψ(HTSP+EVOW+EVOW2) | 207.57 | 12.89 | 0.00 | 1.00 | 5 |
| ψ(LAND) | 211.92 | 17.24 | 0.00 | 1.00 | 3 |
| ψ(HTSP+LAND) | 212.76 | 18.08 | 0.00 | 1.00 | 4 |
| ψ(EVOW+LAND) | 212.97 | 18.29 | 0.00 | 1.00 | 4 |
| ψ(HTSP+EVOW+LAND) | 213.26 | 18.58 | 0.00 | 1.00 | 5 |
| ψ(HTSP+EVOW) | 213.38 | 18.70 | 0.00 | 1.00 | 4 |
| ψ(.) | 213.69 | 19.01 | 0.00 | 1.00 | 2 |
| ψ(EVOW) | 213.82 | 19.14 | 0.00 | 1.00 | 3 |
| ψ(HTSP) | 214.01 | 19.33 | 0.00 | 1.00 | 3 |

[a] Models are denoted as additive (+) and/or multiplicative (*); Variables are defined in Table 3.1.

[b] Akaike's Information Criterion.

[c] Difference in AICc relative to smallest value.

[d] Akaike's weight of models.

[e] Number of parameters.